Dynamic behaviors of the Ricker population model under a set of randomized perturbations

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Abstract

We studied the dynamics of the Ricker population model under perturbations by the discrete random variable $\varepsilon$ which follows distribution $P\{\varepsilon = a_i\} = p_i$, $i = 1, \ldots, n$. $0 < a_i < 1$, $n \geqslant 1$. Under the perturbations, $n + 1$ blurred orbits appeared in the bifurcation diagram. Each of the $n + 1$ blurred orbits consisted of $n$ sub-orbits. The asymptotes of the $n$ sub-orbits in one of the $n + 1$ blurred orbits were $N_t = a_i$ for $i = 1, \ldots, n$. For other $n$ blurred orbits, the asymptotes of the $n$ sub-orbits were $N_t = a_i \exp[r(1 - a_j)] + a_j$, $j = 1, 2, \ldots, n$, for $i = 1, \ldots, n$, respectively. The effects of variances of the random variable $\varepsilon$ on the bifurcation diagrams were examined. As the variance value increased, the bifurcation diagram became more blurred. Perturbation effects of the approximate continuous uniform random variable and random error were compared. The effects of the two perturbations on dynamics of the Ricker model were similar, but with differences. Under different perturbations, the attracting equilibrium points and two-cycle periods in the Ricker model were relatively stable. However, some dynamic properties, such as the periodic windows and the $n$-cycle periods ($n > 4$), could not be observed even when the variance of a perturbation variable was very small. The process of reversal of the period-doubling, an important feature of the Ricker and other population models observed under constant perturbations, was relatively unstable under random perturbations.

Keywords: Chaos; Discrete distribution; Dynamic system; Perturbations; Ricker model; Random error

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1. Introduction

Chaos has been widely found in non-linear population models. However, in population and community experiments, evidence for chaotic dynamics is difficult to confirm [1,2]. The cause of the differences between theoretical models and experimental observations is quite complex. Perturbations have been considered a major cause [3–8]. Study of the dynamics of non-linear population models under perturbed environments is critical to modeling biological and ecological events in the real world.

Some population models are very sensitive to perturbations. McCallum [9] found that migrations could significantly change the properties of population dynamics of the modified Ricker population model, which is as follows:

\[ N_{t+1} = N_t \exp[r(1 - N_t)] + \lambda, \]

in which \( \lambda > 0 \) and \( \lambda \) is a constant representing migration. Stone [10] further studied Eq. (1) and concluded that a seemingly minor constant structural perturbation (\( \lambda \ll 1 \)) could significantly change the dynamics of simple, non-linear difference equations. He confirmed that the period-doubling route to chaos, the essential feature of some simple population models, would break down and suddenly reverse, giving rise to distinctive period-halving bifurcation diagrams. The phenomenon has also been found in other models [11,12]. Although there are population models in which such a property may not exist [13], findings by McCallum [9] and Stone [10] show the possibility of controlling and preventing the onset of chaos by introducing a constant perturbation every generation to the populations whose models have this property [10].

However, the supposition that the perturbation, \( \lambda \), is a constant is very special. In the real world, perturbations could be far more complex. To use constant perturbations to control and prevent the onset of chaos, we would address the following three questions: (1) If in each generation the perturbation randomly takes a value from two values (such as 0.06 and 0.07), what is the result? (2) If in each generation the perturbation randomly takes a value in an interval, such as (0.06, 0.07), what is the result? (3) If the perturbation is not just a constant, but \( \lambda + \varepsilon \), in which \( \varepsilon \) is a random error (normally distributed random variable with variance \( \sigma^2 \) and mean zero), does the perturbation still control and prevent the onset of chaos? Answers to these questions would make the findings by McCallum [9] and Stone [10] more applicable. Since these questions are related to random variables that can characterize a wide range of random events, we need to study the model dynamics under complex perturbations that have properties of randomness. In this paper, we studied dynamics of the Ricker population model under perturbations, which can be described by a set of discrete random variables. We also discussed the stability of the modified Ricker model (Eq. (1)) under random error perturbations and the perturbation caused by approximate continuous uniform random variables. Our results show the complexity of dynamic behaviors, of the simple population model under perturbations of random variables.

2. The model and results

We considered the following model:

\[ N_{t+1} = N_t \exp[r(1 - N_t)] + \varepsilon_{t+1}, \]
in which $\varepsilon_1, \varepsilon_2, \ldots, \varepsilon_t, \varepsilon_{t+1}, \ldots$ are independent and identically distributed (i.i.d.) discrete uniform random variables with the distribution of $P(\varepsilon = a_i) = p_i$, $i = 1, \ldots, n$, $0 < a_i \ll 1$, $n \geq 1$. Under this supposition, a perturbation (such as a migration) occurs in every generation valued by one of the $a_i$s with the probability $p_i$. When $\varepsilon_i$s are considered as i.i.d. random variables with distribution $N(\lambda, \sigma^2)$, Eq. (2) corresponds to Eq. (1) under random error perturbations.

2.1. Bifurcation diagrams of the population dynamic system

For simplification of discussion, we supposed $p_i = 1/n$ in this paragraph to discuss the bifurcation diagram of Eq. (2). Two special cases of the discrete random variable defined by Eq. (2) are as follows: (1) $n = 1$, $a_1 = 0$, and (2) $n = 1$, $a_1$ is a constant, $0 < a_1 \ll 1$. The first case corresponds to the original Ricker model which has no perturbation ($\lambda = 0$ for Eq. (1)). Case 2 corresponds to Eq. (1), the modified Ricker model that has constant perturbation. The bifurcation diagrams of the two cases are well known [10]. Under more general suppositions on the discrete variables $\varepsilon_i$s, the bifurcation diagrams of Eq. (2) are quite different from those of the two special cases. Fig. 1 contains bifurcation diagrams corresponding to the following four suppositions on $\varepsilon_i$ in Eq. (2): (1) $a_1 = 0.03$, $a_2 = 0.06$; (2) $a_1 = 0.04$, $a_2 = 0.06$; (3) $a_1 = 0.03$, $a_2 = 0.04$, $a_3 = 0.06$; and (4) $a_i = 0.01 \times i$ for $i = 1, \ldots, 10$. Under these perturbations, the well-known features of the period-doubling to chaos of the Ricker model are no longer present, and the feature of period-doubling

![Fig. 1. Diagrams of the Ricker model under perturbations: $N_{i+1} = N_i \exp[r(1 - N_i)] + \varepsilon_{i+1}$, in which $\varepsilon_1, \varepsilon_2, \ldots, \varepsilon_{t+1}, \ldots$ were i.i.d. variables with the distribution $P(\varepsilon = a_i) = 1/n$, for $i = 1, \ldots, n$: (a) $n = 2$, $a_1 = 0.03$, $a_2 = 0.06$; (b) $n = 2$, $a_1 = 0.04$, $a_2 = 0.06$; (c) $n = 3$, $a_1 = 0.03$, $a_2 = 0.04$, and $a_3 = 0.06$; (d) $n = 10$, $a_i = 0.01, 0.02, \ldots, 0.1$, for $i = 1, \ldots, 10$. The $r$ changed from 0.01 to 5 with an increment of 0.01. For each $r$, the respective equation was iterated 700 times and results of the last 200 times were plotted. $N_0 = 0.75$. Maps were omitted when $r$ was (0.5, 1.5) since it was similar to [0.4,0.5].]
reversals of the Ricker model under a constant perturbation found by McCallum [9] and Stone [10] were changed. There were chaotic regimes with blurred orbits appearing in the bifurcation diagrams. With an increase in the $r$ value, the blurred orbits became clear (Fig. 1). For $n \geq 1$, $a_i > 0$, and $i = 1, \ldots, n$, the number of blurred orbits equaled $n + 1$. The blurred orbit in the lowest position was found in all sub-figures of Fig. 1. As long as $n \geq 1$ and $a_i > 0$, this orbit appeared. The positions of other orbits were determined by the values of $a_i$, and not affected by the parameter $n$. For example, positions of the top orbit for Fig. 1(a)–(c) all corresponded to $a_i = 0$; $i = 1, \ldots, 10$, the number of blurred orbits equaled $n = 10$. The blurred orbit in the lowest position was found in all sub-figures of Fig. 1. As long as $n \geq 1$ and $a_i > 0$, this orbit appeared. The positions of other orbits were determined by the values of $a_i$ ($i = 1, \ldots, 10$), and not affected by the parameter $n$. For example, positions of the top orbit for Fig. 1(a)–(c) all corresponded to $a_i = 0$: $i = 1, \ldots, 10$. In Fig. 1(c), the middle two orbits corresponded to $a_i = 0$: $i = 2, 3, 4$. For the middle two orbits, the lower one had the same position as the middle orbit in Fig. 1(a). The higher one had the same position of the middle orbit of Fig. 1(b).

To investigate blurred orbits, the population values ($N$) were plotted in logarithmic scale. For all sub-figures of Fig. 1, the orbits at the lowest position actually consisted of $n$ periodic orbits. For example, when $n = 10$, $a_1 = 0.01$, and $a_i = 0.02, \ldots, 0.1$ for $i = 1, \ldots, 10$ (comparison of Fig. 1(d)). Asymptotes for the 10 blurred orbits above log ($N$) = 0 are $N_i = a_i \exp [r(1 - a_i)] + e_i$ ($i = 1, \ldots, 10$), and the 10 orbits under log ($N$) = 0 are $N_i = a_i$ ($i = 1, \ldots, 10$), respectively. The value of $r$ changed from 1.5 to 6 with an increment of 0.01. For each $r$, the respective equation was iterated 700 times and results of the last 200 times were plotted. $N_0 = 0.75$.
orbits in an \(N\)–\(r\) coordinate system (Fig. 1(a)). In a \(\log(N)\)–\(r\) coordinate system, the orbit corresponding to the lowest orbit in Fig. 1(a) actually consisted of two sub-orbits (Fig. 2(a)). When \(n \hat{=}_{10}\) and \(a_i \hat{=}_{01}; 02; \ldots; 09; 1\), the bifurcation diagram had 11 orbits in an \(N\)–\(r\) coordinate system (Fig. 1(d)). In a \(\log(N)\)–\(r\) coordinate system, the blurred orbit in the lowest position consisted of 10 sub-orbits (Fig. 2(b)).

To examine other blurred orbits, part of the bifurcation diagram of Fig. 2(a) was enlarged as shown in Fig. 3. When \(r\) was sufficiently large, the blurred orbits A and B in Fig. 2(a) also had two sub-orbits. Combining the results of Figs. 2(a) and 3, we concluded that in Fig. 1(a) all three blurred orbits had two sub-orbits. In fact, this is a common property of Eq. (2). The mathematical analysis in the following paragraph shows that in an \(N\)–\(r\) coordinate system, there are \(n\) blurred orbits in the bifurcation diagram for Model 2 (Eq. (2)), when \(r\) is sufficiently large with each of the \(n+1\) orbits consisting of \(n\) sub-orbits.

2.2. Interaction between the orbits, parameters \(a_i\) and probabilities \(p_i\) in Eq. (2)

The above results were obtained by computer simulation. However, by mathematical analysis, we found more detailed properties of the \(n+1\) orbits of Eq. (2). The results are summarized in Theorem 2.1 as follows:

**Theorem 2.1.** When \(r\) is sufficiently large, there are \(n(n+1)\) blurred orbits in Eq. (2). The asymptotes of the \(n(n+1)\) blurred orbits can be divided into \(n+1\) groups, \(G(0)\) and \(G(i)\), for \(i = 1, \ldots, n\). In group \(G(0)\), the \(n\) asymptotes of the blurred orbits are \(N_i = a_i, i = 1, \ldots, n\); and in group \(G(i)\), the asymptotes are \(N_i = a_i \exp[r(1 - a_i)] + a_j, j = 1, 2, \ldots, n\), for \(i = 1, \ldots, n\).
To prove Theorem 2.1, we need the following four conclusions:
1. \( N_t \exp [r(1 - N_t)] \to 0 \) when \( N_t > 1 \) and \( r \to \infty \),
2. \( N_t \exp [r(1 - N_t)] \to \infty \), when \( 0 < N_t < 1 \) and \( r \to \infty \),
3. \( rN_t \exp [r(1 - N_t)] \to 0 \), when \( N_t > 1 \) and \( r \to \infty \), and
4. the population density of \( N_t \exp [r(1 - N_t)] + \epsilon_t \) will take values larger than 1 for infinite times when \( t \to \infty \) and when \( r \) is sufficiently large.

The first two conclusions are easy to verify. Conclusion 3 can be obtained by using L'Hospital's rule as follows:

\[
\lim_{r \to \infty} rN_t \exp [r(1 - N_t)] = N_t \lim_{r \to \infty} \frac{dr}{dr} \exp [-r(1 - N_t)]
\]
\[
= N_t \left( \frac{dr}{dr} \exp [-r(1 - N_t)] \right)_{r \to \infty}
\]
\[
= [-N_t/(1 - N_t)] \lim_{r \to \infty} \{1/\exp [-r(1 - N_t)]\}
\]
\[
= [-N_t/(1 - N_t)] \lim \exp [r(1 - N_t)]
\]
\[
= 0.
\]

Conclusion 4 can be obtained by using Conclusion 2. The following are two possibilities that the series \( \{N_t\} \) will take when \( t \) goes to infinity: (1) \( N_t = 1 \) will appear for infinite times; and (2) \( N_t = 1 \) will appear for infinite times. If \( N_t = 1 \), then \( N_{t+1} = N_t \exp [r(1 - N_t)] + \epsilon_{t+1} = 1 + \epsilon_{t+1} > 1 \). So, if \( N_t = 1 \) appears infinite times when \( t \to \infty \), \( N_t > 1 \) will also appear for infinite times; otherwise if \( N_t = 1 \) only appears for limited times, then at least \( N_t > 1 \) or \( N_t < 1 \) will appear for infinite times when \( t \to \infty \). If \( N_t > 1 \) will appear for infinite times, Conclusion 4 holds. If \( N_t < 1 \) appears for infinite times, because of Conclusion 2, \( N_{t+1} \) will be larger than 1 when \( r \) is sufficiently large, so \( N_t > 1 \) will also appear for infinite times.

**Proof of Theorem 2.1.** If \( N_t > 1 \) and \( r \) is sufficiently large, \( N_{t+1} = N_t \exp [r(1 - N_t)] + \epsilon_{t+1} \) can be expressed using Conclusion 1 as \( N_{t+1} = \delta(r, N_t) + \epsilon_{t+1} \), in which \( \delta(r, N_t) = N_t \exp [r(1 - N_t)] \to 0 \), when \( r \to \infty \). Because \( \epsilon_{t+1} \) will take one of the values of \( a_1, a_2, \ldots, a_n \) with the probability \( p_i \), we can suppose \( N_{t+1} = a_i + \delta(r, N_t) \). By substituting \( N_{t+1} = a_i + \delta(r, N_t) \) into Eq. (2), we obtained

\[
N_{t+2} = [a_i + \delta(r, N_t)] \exp \{r[1 - (a_i + \delta(r, N_t))]\} + \epsilon_{t+2}
\]
\[
= [a_i + \delta(r, N_t)] \exp [r(1 - a_i)] \exp [-r\delta(r, N_t)] + \epsilon_{t+2}
\]
\[
= a_i \exp [r(1 - a_i)] \exp [-r\delta(r, N_t)] + \delta(r, N_t) \exp [r(1 - a_i)] \exp [-r\delta(r, N_t)] + \epsilon_{t+2}
\]

Since \( r\delta(r, N_t) \to 0 \) (Conclusion 3), \( \exp [-r\delta(r, N_t)] \to 1 \), when \( r \to \infty \). Then

\[
N_{t+2} \to a_i \exp [r(1 - a_i)] + \delta(r, N_t) \exp [r(1 - a_i)] + \epsilon_{t+2}(r \to \infty)
\]
\[
= a_i \exp [r(1 - a_i)][1 + \delta(r, N_t)/a_i] + \epsilon_{t+2}(r \to \infty).
\]

As \( \delta(r, N_t) \to 0 \) and \( a_i \) is a constant, \( \delta(r, N_t)/a_i \to 0 \), when \( r \to \infty \), consequently,

\[
N_{t+2} \to a_i \exp [r(1 - a_i)] + \epsilon_{t+2}, \text{ when } r \to \infty.
\]
The above analysis shows that if \( N_t > 1 \), \( N_{t+1} \) will converge to \( a_i \) and \( N_{t+2} \) will converge to 
\[ a_i \exp [r(1 - a_i)] + \epsilon_t + \epsilon_{t+2}. \]
Because \( N_t > 1 \) will appear for infinite times when \( t \to \infty \) (Conclusion 4),
\( N_t = a_i \) and \( N_t = a_i \exp [r(1 - a_i)] + \epsilon_t \) are asymptotes of the blurred orbits. Since \( \epsilon_t \) can take \( n \) different values, \( a_1, a_2, \ldots, a_n, N_t = a_i \exp [r(1 - a_i)] + \epsilon_t \) consists of \( n \) asymptotes of orbits,
\( N_t = a_i \exp [r(1 - a_i)] + a_j, j = 1, 2, \ldots, n. \) If we use \( G(i) \) to denote the asymptote group
\( N_t a_i \exp [r(1 - a_i)] + \epsilon \), the above analysis also shows that if \( N_{t+1} \) is located to orbit \( N_i = a_i, N_{t+2} \) must be located to one of the asymptote orbits in \( G(i), N_t = a_i \exp [r(1 - a_i)] + a_j (j = 1, \ldots, n) \) with probability \( p_j \).

When \( N_{t+2} \) is located to the asymptote orbit \( N_{t+2} = a_i \exp [r(1 - a_i)] + a_j, \) because \( 0 < a_i \), and
\( a_j < 1, a_i \exp [r(1 - a_i)] \to \infty \) when \( r \to \infty \) (Conclusion 2). So when \( r \) is sufficiently large, \( N_{t+2} \) should be greater than 1. Then we have
\( \delta(r, N_{t+2}) = N_{t+2} \exp [r(1 - N_{t+2})] \to 0, \) when \( r \to \infty \)
(Conclusion 1). So \( N_{t+3} = \delta(r, N_{t+2}) + \epsilon_{t+3} \to \epsilon_{t+3}, \) when \( R \to \infty \). Because \( \epsilon_{t+3} \) will take the value of
\( a_i \) for \( i = 1, \ldots, n \) with probability \( p_i, N_{t+3} \) will be located to the asymptote \( N_t = a_i \) with probability \( p_i \) for \( i = 1, \ldots, n. \)

If \( G(0) \) denotes the asymptote group \( N_t = a_i, i = 1, \ldots, n, \) then there are \( n + 1 \) asymptote orbit
groups for Eq. (2), \( G(0), G(1), \ldots, G(n). \) If \( G(i, j) \) denotes asymptote orbit \( N_t = a_i, j, \) and \( G(i, j) \)
denotes the asymptote orbit \( N_t = a_i \exp [r(1 - a_i)] + a_j, j = 1, 2, \ldots, n, i = 1, \ldots, n, \) then the above analysis shows that when \( r \) is sufficiently large, \( N_t \) eventually will be located in one of the \( n(n + 1) \) orbits. If \( N_t \) is located in \( G(0, i), N_{t+1} \) will be located to \( G(i, j) \) with probability \( p_j \) for
\( j = 1, \ldots, n \); if \( N_t \) is located in \( G(i, j), N_{t+1} \) will be located to \( G(0, i) \) with probability \( p_i \) for
\( i = 1, \ldots, n. \)

When \( n = 2, a_1 = 0.03, a_2 = 0.06, \) two orbits (A' and B') and two blurred orbits (A and B)
can be seen (Fig. 2(a)). According to Theorem 2.1, the asymptote of orbit A' is \( N_t = 0.03 \) (or
\( \log(N) = \log(0.03) = -3.5066) \), and that of B' is \( N_t = 0.06 \) (or \( \log(N) = \log(0.06) = -2.8134 \)).
The blurred orbit A consists of two sub-orbits and the asymptotes of the two sub-orbits are
\( N_t = 0.03 \exp [r(1 - 0.03)] + 0.03 \) and \( N_t = 0.03 \exp [r(1 - 0.03)] + 0.06; \) and the blurred orbit B
consists of two sub-orbits and the two asymptotes are \( N_t = 0.06 \exp [r(1 - 0.06)] + 0.03 \) and
\( N_t = 0.06 \exp [r(1 - 0.06)] + 0.06. \) When \( N_t \) is located in A', \( N_{t+1} \) must be located in one of the two
orbits in A, and if \( N_t \) is located in B', \( N_{t+1} \) must be located in one of the two orbits in B. If \( N_t \)
is located in A or B, then \( N_{t+1} \) will be located to A' or B' with probability \( p_1 \) or \( p_2 \) when
\( P(\epsilon_i = 0.03) = p_1 \) and \( P(\epsilon_i = 0.06) = p_2 \), respectively. However, the asymptotes are only
determined by \( a_i, \) not by \( p_i. \) For example, when the variable \( \epsilon_i \) in Eq. (2) has the distribution
\( p_1 = P(\epsilon_i = 0.03) = 0.75, p_2 = P(\epsilon_i = 0.06) = 0.25, \) then the bifurcation diagram of Eq. (2) is the
same as Fig. 1(a) (or Fig. 2(a under the logarithmic scale), which corresponds to the distribution of
\( P(\epsilon_i = 0.03) = 0.5 \) and \( P(\epsilon_i = 0.06) = 0.5. \) The effect of the difference between the two distributions on the dynamic behaviors of Eq. (2) is that the rate of the numbers \( N_t \), located to orbits
A' (A) and B' (B) is about 3:1 when the distribution of \( \epsilon_i \) is \( P(\epsilon_i = 0.03) = 0.75 \) and
\( P(\epsilon_i = 0.06) = 0.25, \) and about 1:1 when the distribution of \( \epsilon_i \) is \( P(\epsilon_i = 0.06) = 0.5, \)
\( P(\epsilon_i = 0.03) = 0.5. \)

A direct application of Theorem 2.1 is the following corollary, which gives the equations of the
asymptote orbits of the population model \( N_{t+1} = (N_t \exp [r(1 - N_t)] + \lambda, 0 < \lambda \ll 1. \)

**Corollary 2.1.** When \( n = 1, \epsilon_i = \lambda \) in Eq. (2). It is equivalent to Eq. (1), the Ricker model under
constant perturbations. In this case, the two asymptote orbits of the model are as follows:
\[ N_t = \lambda_t \quad \text{and} \quad N_t = \lambda_t \exp[r(1 - \lambda)] + \lambda. \]

When \( \lambda = 0.06 \), the two asymptote orbits are \( N_t = 0.06 \) and \( N_t = 0.06 \exp[r(1 - 0.06)] + 0.06 \).

Refer to Stone’s Fig. 1(b) [10] for the curves of the two asymptote orbits. When \( r \) is sufficiently large, such as \( r > 3.8 \), the system will take the value of \( \lambda \) or \( \lambda \exp[r(1 - \lambda)] + \lambda \) alternatively.

2.3. Effects of variances of the discrete uniform random variable perturbations on dynamics

The variance is an important parameter characterizing random variables. When a random variable is considered as a perturbation, small variance of the variable means the deviation of perturbations between different generations is small, and vice versa. The effects on the random variables of Eq. (2) under different variances are compared by considering the following three cases:

1. \( P(\varepsilon_t = 0.02 + 0.004 \times j) = 1/21 \), \( j = 0, \ldots, 20 \).
2. \( P(\varepsilon_t = 0.04 + 0.002 \times j) = 1/21 \), \( j = 0, \ldots, 20 \).
3. \( P(\varepsilon_t = 0.05 + 0.001 \times j) = 1/21 \), \( j = 0, \ldots, 20 \).

The mean value \( (E(\varepsilon_t)) \) of each of the three variables is 0.06. The variances in the three cases are 0.024\(^2\), 0.012\(^2\), and 0.0061\(^2\), respectively. Fig. 4(a) and (b) shows that if the variance of \( \varepsilon_t \) is large, the bifurcation diagram will be quite different from that of the \( N_{t+1} = N_t \exp[r(1 - N_t)] + E(\varepsilon_t) \) (Fig. 4(c)). Compare Fig. 1(b) of Stone [10] with Fig. 4(a)–(c) in this paper to see the effects of different variances.

2.4. Comparison of effects of discrete uniform perturbations and random error perturbations

Fig. 4(d) is the bifurcation diagram of Eq. (2) under the supposition that \( \varepsilon_t \sim N(0.06, 0.0061^2) \). It can be compared with Fig. 4(c) to see the differences between the perturbations caused by the two kinds of random variables, the discrete uniform random variables and the random error perturbation. The mean and the variance of the variables considered in Fig. 4(c) and (d) are the same, mean \( E(\varepsilon_t) = 0.06 \) and variance \( \sigma^2 = 0.0061^2 \). The difference is that the discrete uniform distribution is distributed in the interval \([0.05, 0.07]\) but the normal distribution variable is distributed in \((-\infty, \infty)\). The difference between the two bifurcation diagrams is that the bounds of the bifurcation diagram in Fig. 4(c) are smoother than that of Fig. 4(d). If the normal distribution is truncated to make \( \varepsilon_t \) distributed in the interval \([0.05, 0.07]\), i.e., we let \( \varepsilon_t \sim N(0.06, 0.0061^2) \) with the condition that if \( \varepsilon_t < 0.05 \) we let \( \varepsilon_t = 0.05 \), and if \( \varepsilon > 0.07 \) we let \( \varepsilon_t = 0.07 \), then the bifurcation diagrams of Eq. (2) are very close to that of Fig. 4(c).

Here the normal variable \( N(0.06, 0.0061^2) \) is constructed by the central limit theorem [14]. It would be interesting to compare the effect on dynamics of a normal variable and a continuous uniformly distributed random variable because the latter is a very important random variable in biological study, and is one of the three questions we proposed in the first paragraph. However, using a computer, we can only construct approximate continuous uniform random variables. For example, suppose random variable \( \xi \) is a continuous uniform random variable distributed in the interval \([0,1]\). The variable \( \xi \) cannot be constructed directly. We can only
make discrete uniform random variables \( \xi_n \) with the distribution \( P(\xi_n = i/n) = 1/n, \) \( i = 0, \ldots, n, \) in which \( n \) is an integer to approach \( \xi. \) In fact \( \{\xi_n\} \) converges in probability to \( \xi \) [15,16]. In Eq. (2), if the perturbation variable is \( \xi_n, \) no matter how larger the number \( n \) is, the \( n(n + 1) \) asymptote orbits described in Theorem 2.1 exist even though the orbits might not be clear enough to distinguish in diagrams where \( n \) is sufficiently large (for example, \( n > 50 \)). If the perturbation variable is \( \xi, \) the continuous uniform random variable, there should be no such blurred orbits because the conditions to produce the orbits no longer exist. However, the diagrams of the Ricker model under the perturbation of a continuous uniform random variable can be approached by the discrete uniform random variable. When the parameter \( n \) in the discrete uniform random variable is sufficiently large and the interval \([a, b]\) in which the continuous uniform random variables are defined is small enough, the discrete uniform random variable can be taken as an approximate continuous uniform random variable defined in \([a, b]\). For example, Fig. 4(c) can be taken as a diagram of Eq. (2) in which the perturbation random variable is an approximate continuous uniform variable distributed in the interval \([0.05, 0.07]\) because the interval is very small and \( n = 21 \) is sufficiently large in comparison with the interval.

2.5. Biological interpretation

Our analysis shows that when \( r \) is sufficiently large, the dynamic system defined by Eq. (2) will be eventually located to the orbits described by Theorem 2.1. What are the biological implica-
tions? We answer the question first by examining the biological meaning of constant perturbation. For the model corresponding to Eq. (1), there are two asymptote orbits which are \( N_t = \hat{\lambda}, \) and \( N_t = \hat{\lambda} \exp[r(1 - \hat{\lambda})] + \hat{\lambda}. \) When \( \hat{\lambda} = 0.06, \) the asymptotes are \( N_t = 0.06, \) and \( N_t = 0.06 \exp[r(1 - 0.06)] + 0.06. \) When \( r \) is sufficiently large, the population takes values of the two asymptotes, alternatively. For example, when \( r = 4 \)

\[
N_t = 0.06 \exp[4 \times (1 - 0.06)] + 0.06 = 2.64 \quad \text{and}
\]

\[
N_{t+1} = 2.64 \exp[4 \times (1 - 2.64)] + 0.06 \approx 0.06.
\]

A time series of \( N_t \) would be 0.06, 2.64, 0.06, 2.64, 0.06, 2.64, \ldots, when generation number \( t \) is sufficiently large. The ecological interpretation of the above pattern of the dynamic system could be as follows: a site is colonized by a small number of immigrants \( (N_t = 0.06), \) the next generation overshoots the equilibrium \( (N_t = 2.64); \) and by the third generation may become extinct if there are no new immigrants. Such kind of population dynamics exists in the real world, especially to some migrating insect and airborne pathogen populations. One example is migrating wheat aphids, an agricultural pest [17,18]. In some winter wheat production regions, the amount of the local overwintering population is low because few aphids survive the winter in cold regions. The major portion of the initial population in spring, which is low in density, migrates from the places where they overwinter. When weather favors aphids growth in summer, the population will increase with high reproduction. After wheat harvest, most aphids populations migrate and only a few that remain survive the winter. Such dynamics repeats year after year and is common in northern winter wheat production regions in China [19].

Another example of this type of population dynamics is annual dynamics of *Puccinia striiformis*, a fungal pathogen causing stripe rust disease of wheat in central and northern China. In Chinese wheat production regions, the fungus can survive and grow all year round in mountainous northwest wheat production regions. The fungus cannot survive over summer in the northeastern and central wheat production regions. In these regions, annual epidemics start with airborne spores moved in by air current from northwestern wheat production regions. The initial level of infestation depends on the density of exotic airborne spores [20,21].

Three common points can be made of the dynamics in the examples above: (1) the populations early in the growing season are migrant populations; (2) rates of pest increase are high; and (3) the level of the migrating population is independent of the density of the local population. This kind of population dynamics seems to fit the dynamic properties of the model well. If Eq. (1) or (2) is used to describe such dynamics, a time unit \( t \) will be a growing season of the host instead of a generation of the pests because of the overlapping between pest generations in a growing season.

If pest immigration is constant every growing season, Eq. (1) could be used to describe the dynamics of this pest; if immigration of a pest is nearly a constant, Eq. (2) can be used with a perturbation term \( \varepsilon_t \) that could be a normal variable \( N(\hat{\lambda}, \sigma^2). \) In fact, the constant perturbation \( \hat{\lambda} \) can be taken as a special case of the variable perturbation, \( N(\hat{\lambda}, \sigma^2) \) where \( \sigma = 0. \) If the immigration of a pest has different possible levels, Eq. (2) could be used with a perturbation term \( \varepsilon_t \) that could be a random variable with the distribution \( P\{\varepsilon = a_i\} = p_i, i = 1, \ldots, n, \) \( 0 < a_i \ll 1, n \geq 1. \) If immigration varies within a small interval \( [a, b], \) an approximate continuous random variable can be used.
3. Discussion

The distribution of $P\{e_i = a_i\} = p_i$, $i = 1, \ldots, n$, $a_i > 0$, $n \geq 1$, covers almost all the discrete distribution. When $n \to \infty$, the variable $e_i$ takes a countable number of values, such as in a Poisson distribution, negative binomial distribution, or geometric distribution. When $n$ is a real integral number, the variable $e_i$ takes a finite number of values, such as in a binomial distribution or hypergeometric distribution [22]. Because the orbits in the dynamic diagram of Eq. (2) were determined by $a_i$ and were not related to the value of $p_i$, our findings on the dynamics of Eq. (2) are of general implication.

All our simulation results presented in Figs. 1, 2, and 4 show that the attracting equilibrium points ($r < 2$) and the two-cycle periods ($2 < r < 2.6924$) are relatively stable under both kinds of perturbations. The process of reversals of the period-doubling of Eq. (1) under a constant perturbation [10] is not as stable as the attracting equilibrium points and the two-cycle periods under random error perturbations. Fig. 4(d) was the diagram of equation $N_{t+1} = N_t \exp[r(1 - N_t)] + 0.06 + e_t$ with $e_t \sim (0, 0.0061^2)$. The deviations of the system at the attracting equilibrium ($r < 2$) and the two-cycle periods ($2 < r < 2.6924$) were very small. The deviations become quite large when the process of reversals of the period-doubling begin to appear ($r > 3.5$) (Fig. 4(d)) although the variance of the random variable is very small. To compare the effects of random error with a larger variance, we ran the model $N_{t+1} = N_t \exp[r(1 - N_t)] + 0.06 + e_{t+1}$ under the supposition of $e_t \sim N(0, \sigma^2)$ with $\sigma = 0.024$. The attracting equilibrium ($r < 2$) was stable at that perturbation level but the process of reversals of the period-doubling that happen under constant perturbations was destroyed completely. Our simulation suggests that if we use constant perturbation to control chaos, we must control the random error (also referred to as noise). If the variance of the random error can be controlled, using constant perturbation to control chaos would be applicable as indicated by Fig. 4(d).

In this paper, we only consider the simplest case, in which the perturbations $\{e_t\}$ are i.i.d. random variables and independent from the population density. Such type of perturbations commonly exists in the real world [3,23]. There are other kinds of perturbations that have been considered, such as the density dependent [24,25] as well as considering the parameters of population equations as random variables [26]. Different suppositions on perturbation terms have different biological meanings, and would result in different dynamic behaviors of population models.

It is unknown if the properties of the Ricker model that were demonstrated under perturbation by the random variable defined in Theorem 2.1 also exist in other population models. Even with constant perturbations, no criteria are available to examine a model for the property found by Stone [10]. Development of such mathematical criteria would be a significant extension of our current findings. At present, we can just guess that a model that has the property described by Stone [10] should have the properties defined by Theorem 2.1 in this paper because Eq. (2) is an extension of Eq. (1).

The pioneering work by McCallum [9] and Stone [10] suggests the importance of studying the dynamic behaviors of a population model under perturbations. Such studies are useful extensions in the methodology of population modeling and make modeling approach the real world. We studied the dynamic behaviors of the host-parasite interaction model under perturbations and uncovered some important properties [8,27]. Under the perturbations, the dynamics of ecological
or biological systems become more complex and difficult for analytical approach. However, computer simulation is a powerful tool in the analysis of dynamic systems [28–30], and the combination of computer simulation with mathematical and statistical analysis would enhance our analytical power [31]. The Ricker model is a simple population model. Even a simple population model could have very complex dynamic behaviors under randomized perturbations. Therefore, to make our model more close to the real world it is necessary to examine deterministic properties of some population models under randomized perturbations.

References