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Hopf bifurcation of basic food web of species based on standard normal theory

Puyi Lam Kai-shek

School of Mathematics and Physics, China University of Geosciences, Wuhan, 430074, PR China.

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In this paper, we analyze the Hopf bifurcation of basic food web of four species based on standard normal form theory. The basic model we consider is owed to a bottom prey X, two competing predators Y and Z on X, and a super-predator W only on Y. It is found that periodic solutions arise from the main parameter values δ_1 and ζ through through a Hopf bifurcation point. The direction and type of the Hopf bifurcation involved as well as the parameter values also are determined.

Key words: Chaos, bifurcation analysis, food web, prey-predator, four-dimensional.

INTRODUCTION

Chaos theory is a field of study in applied mathematics, and it has applications in several disciplines including physics, economics, biology and philosophy. It has always intertwined with complex population dynamics since its inception (Xiang et al., 2011). The question of under what minimum circumstance can chaos arises in population models was raised which postulates that it requires at the minimum the coupling of two oscillators from some shorter predator-prey chains (Rai, 2004). The main objective of this paper is to show that this hypothesis is false for a food web of four species in which chaos can occur even though none of the sub-chains contains any oscillator.

Bockelman et al. (2004) addressed an important issue in population dynamics. The competition exclusion principle presented by Koch (1974), Armstrong and McGehee (1980) and Waltman (1983), which states that for most systems where two predators feed on a prey there cannot be any stable coexisting state. The chaotic four species model found in their paper is not by an exclusive singular perturbation construction as with the case of Liu et al. (2003). Instead, it is found by a combination of singular perturbation analysis, Hopf bifurcation analysis and a numerical bifurcation study on a period-doubling cascade originated from the Hopf point. Understanding the system mechanism that creates this phenomenon is particularly challenging because it seems that the singular perturbation approach alone is not thoroughly effective.

The food web includes X for the prey, Y, Z for the competing predators of the common prey X, and W for the top-predator on Y. We will assume that X is governed by Verhulst's logistic growth principle proposed by Lotka (1925) and Volterra (1926) in the absence of the predators, and all predators governed by Holling's Type II predation functional form, two of the most fundamental modeling principles in ecology. The dimensional model is as follows:

$$\begin{aligned}
\frac{dX}{d\tau} &= rX\left(1-\frac{X}{K}\right) - \frac{p_1 X}{H_1+X} - \frac{p_2 X}{H_2+X},\\
\frac{dY}{d\tau} &= \frac{b_1 p_1 X}{H_1+X}Y - d_1 y - \frac{p_3 Y}{H_3+Y}W,\\
\frac{dZ}{d\tau} &= \frac{b_2 p_2 X}{H_2+X}Z - d_2 Z,\\
\frac{dW}{d\tau} &= \frac{b_3 p_3 Y}{H_3+Y}W - d_3 W,
\end{aligned} \quad (1)$$

Here *r* is the intrinsic growth rate and and *K* is the carrying capacity for the prey. Parameter p_1 is the maximum predation rate per predator *Y* and H_1 is the semi-saturation density for which when *X* = H_1 the Y's

*Corresponding author: E-mail: lam_puyi22@yahoo.co.uk

predation rate is half of its maximum, $p_1/2$. Parameter b_1 is predator Y's birth-to-consumption ratio and d_1 is its per-capita death rate. The remaining parameters have parallel and analogous meanings. Using the scaling transformations together with the dimensionless parameters (Rai, 2004), Equation 1 is changed to this form:

$$
\begin{aligned}
\zeta \frac{dx}{dt} &= x\left(1 - x - \frac{y}{\beta_1 + x} - \frac{z}{\beta_2 + x}\right),\\
\frac{dy}{dt} &= y\left(\frac{x}{\beta_1 + x} - \delta_1 - \frac{w}{\beta_3 + y}\right),\\
\frac{dz}{d\tau} &= \varepsilon_1 z\left(\frac{x}{\beta_2 + x} - \delta_2\right),\\
\frac{dw}{d\tau} &= \varepsilon_2 w\left(\frac{x}{\beta_2 + y} - \delta_3\right),
\end{aligned}
\qquad (2)
$$

where all the parameters are positive. Its chaotic dynamics and the routes to chaos are observed by numerical simulations (Wei, 2010). It has been studied for the existence of a chaotic attractor (Bockelman et al., 2004), on which all species coexist, by using a geometric method of singular perturbations. It is shown that under the situation that without the top-predator *W*, competitor *Z* goes to extinction, without *Z* the *XYW* locks in a periodic cycle, yet with all species, the noncompetitive *Z* can derive the dynamics from periodic orbits to chaos.

Bockelman and Deng (2005) have shown that a one-dimensional bifurcation diagram using the relative reproduction rate of *Z* as the bifurcation parameter was computed to show period-doubling cascades leading to chaos. The chaotic attractor is formed via period-doubling cascades from a Hopf bifurcation point. The results of Hopf bifurcation were not proved analytically. All the conditions of the Hopf bifurcation theorem were not verified and stability of the limit cycle were not addressed. Moreover, to the best of our knowledge, there are few reports on the limit cycle of food web of four species theoretically, while some detailed investigations and studies of dynamical behaviors 3D autonomous systems were given by Yu and Zhang (2004), Dias et al. (2010), Mello et al. (2008) and Wei and Yang (2011). It motivated a great deal of interest to investigate the formation mechanism of chaos and periodic orbit. In this paper, applying the normal from theory introduced by Hassard et al. (1982), we investigated that periodic solutions arise from through a Hopf bifurcation point. The direction and type of the Hopf bifurcation involved as well as the parameter values also are determined.

LOCAL STABILITY AND HOPF BIFURCATION

First, we study the conditions for the existence of the equilibria. Equation 2 have eight possible equilibria labelled by P_i, i=1,2,3,4,5,6a,6b,7, as shown in Table 1 (Wei, 2010). The notations $(x_{P_i}, y_{P_i}, z_{P_i}, w_{P_i}), E_{P_i}$, and A($P_i$) will be used for the coordinates, region of existence and Jacobian matrix of steady state P_i, respectively, throughout this paper.

We choose here to study $P_3\left(\frac{\delta_1\beta_1}{1-\delta_1}, (1-x)(\beta_1+x), 0, 0\right)$, because it seems more meaningful to proceed in the neighbourhood of $z = 0$ and $w = 0$ if we keep in mind the situation of biological interest. It is easy to obtain the condition for the existence of the equilibria P_3, that is, $\{(\delta_1, \beta_1) \mid \delta_1 < 1, \beta_1 > \frac{1-\delta_1}{\delta_1},\}$. The Jacobian matrix of Equation 2, evaluated at P_3, is denoted A(P_3).

Obviously, linearizing Equation 2 about the equilibrium yields the following characteristic equation:

$$
\begin{aligned}
\det(\lambda I - A(P_3)) = {} & (\beta_1+1)\delta_1^3 + \delta_1^2(\beta_1(1-\lambda) - \lambda + 2) + (\delta_1(-\beta_1\lambda + \zeta\lambda^2 + \lambda - 1) - \zeta\lambda^2)\\
& (\beta_1\delta_1((\delta_2-1)\varepsilon_1+\lambda) - \beta_2(\delta_1-1)(\delta_2\varepsilon_1+\lambda))(\beta_1^2\delta_1((\delta_3-1)\varepsilon_2+\lambda) +\\
& \beta_1(\delta_1-1)((\delta_3-1)\varepsilon_2+\lambda) - \beta_3(\delta_1-1)^2(\delta_3\varepsilon_2+\lambda) = 0.
\end{aligned}
\qquad (3)
$$

Now, we study the problem of the existence of Hopf bifurcation.

Theorem 1

Let $\{(\beta_3, \delta_1, \delta_2, \delta_3) \mid \delta_1 < 1, \delta_2 < 1, \delta_3 < 1, \beta_3 > \frac{1-\delta_3}{\delta_3(1-\delta_1^2)\beta_1(1-\delta_1-\delta_1\beta_1)}\}$. When β_1 passes through the critical value $\lambda'(\beta_1)\big|_{\beta_1=\beta_0, \lambda=\omega_0 i} = \frac{\delta_1(\delta_1+1)}{2(\delta_1-1)\zeta} + i\frac{\sqrt{(1-\delta_1^2)\delta_1}}{2(\delta_1-1)\sqrt{\zeta}}\delta_1$, Equation 2 undergoes a Hopf bifurcation at the equilibrium P_3.

Proof

Substituting $\beta_1 = \beta_0 = \frac{1-\delta_0}{1+\delta_1}$ into Equation 3, one can get eigenvalues

Table 1. Possible equilibria in Equation 2, $t \in (0,1)$.

	P_1	P_2	P_3	P_4	P_5
x	0	1	$\frac{\delta_1\beta_1}{1-\delta_1}$	$\frac{\delta_2\beta_2}{1-\delta_2}$	$\frac{\delta_2\beta_2}{1-\delta_2}$
y	0	0	$(1-x)(\beta_1+x)$	0	$t(1-x_p)(\beta_1+x_p)$
z	0	0	0	$(1-x)(\beta_2+x)$	$(1-t)(1-x_p)(\beta_2+x_p)$
w	0	0	0	0	0

	P_{6a}	P_{6b}	P_7
x	$\frac{(1-\beta_1)+\sqrt{(1-\beta_1)^2-4(y-\beta_1)}}{2}$	$\frac{(1-\beta_1)-\sqrt{(1-\beta_1)^2-4(y-\beta_1)}}{2}$	$\frac{\delta_2\beta_2}{1-\delta_2}$
y	$\frac{\delta_3\beta_3}{1-\delta_3}$	$\frac{\delta_3\beta_3}{1-\delta_3}$	$\frac{\delta_3\beta_3}{1-\delta_3}$
z	0	0	$\frac{\beta_2}{1-\delta_2}\left(1-x-\frac{y}{\beta_1+x}\right)$
w	$\frac{x}{(\beta_1+x-\delta_1)}\frac{\beta_3}{1-\delta_3}$	$\frac{x}{(\beta_1+x-\delta_1)}\frac{\beta_3}{1-\delta_3}$	$\frac{\beta_3}{1-\delta_3}\frac{x}{(\beta_1+x-\delta_1)}$

$$\lambda = \pm\sqrt{\frac{(1-\delta_1)\delta_1}{(1+\delta_1)\zeta}}\, i = \pm\omega\, i,$$

$$\lambda_3 = -\frac{(\beta_2\delta_2+\delta_1(-1+\delta_2+\beta_2\delta_2))}{\beta_2+\delta_1+\beta_2\delta_1}\varepsilon_1,$$

$$\lambda_4 = -\frac{(-1+(1+\beta_3(1+\delta_1)^2)\delta_3)}{1+\beta_3(1+\delta_1)^2}\varepsilon_2$$

Then, when

$$\{(\beta_3,\delta_1,\delta_2,\delta_3)\mid \delta_1<1, \delta_2<1, \delta_3<1, \beta_3>\frac{1-\delta_3}{\delta_3(1-\delta_1^2)\beta_1(1-\delta_1-\delta_1\beta_1)}\}'$$

$\lambda_{3,4}<0$ the first condition for Hopf bifurcation in the sense of the theorem (Hassard et al., 1982) is satisfied.

Differentiating all the terms in Equation 3 with respect to the parameter β_1, one obtains

$$\lambda'(\beta_1)|_{\beta_1=\beta_0,\lambda=\omega_0 i} = \frac{\delta_1(\delta_1+1)}{2(\delta_1-1)\zeta} + i\frac{\sqrt{(1-\delta_1^2)\delta_1}}{2(\delta_1-1)\sqrt{\zeta}}\delta_1,$$

which implies

$$\alpha'(0) = \mathrm{Re}(\lambda'(\beta_1))|_{\beta_1=\beta_0,\lambda=\omega_0 i} = \frac{\delta_1(\delta_1+1)}{2(\delta_1-1)\zeta},$$

$$\omega'(0) = \mathrm{Im}(\lambda'(\beta_1))|_{\beta_1=\beta_0,\lambda=\omega_0 i} = \frac{\sqrt{(1-\delta_1^2)\delta_1}}{2(\delta_1-1)\sqrt{\zeta}}\delta_1.$$

Thus, the second condition for a Hopf bifurcation to exist is also met. So, a Hopf bifurcation exists.

DIRECTION AND STABILITY OF BIFURCATING PERIODIC SOLUTIONS

In the following, the stability and expression of the Hopf bifurcation of Equation 2 is investigated by using the normal form theory, some rigorous mathematical analysis, and symbolic computations.

The eigenvectors associated with eigenvalues λ_1, λ_3 and λ_4 will be α_1, α_3 and α_4, respectively. They satisfy

$$A\alpha_1 = i\sqrt{\frac{(1-\delta_1)\delta_1}{(1+\delta_1)\zeta}}\,\alpha_1,$$

$$A\alpha_3 = -\frac{(\beta_2\delta_2+\delta_1(-1+\delta_2+\beta_2\delta_2))}{\beta_2+\delta_1+\beta_2\delta_1}\alpha_3$$

$$A\alpha_4 = -\frac{(-1+(1+\beta_3(1+\delta_1)^2)\delta_3}{1+\beta_3(1+\delta_1)^2}\varepsilon_2\alpha_4.$$

Therefore, one can define

$$T = (\mathrm{Re}\,\alpha_1, -\mathrm{Im}\,\alpha_1, \alpha_3, \alpha_4).$$

Making the transformation $(x, y, z, w)' = T(u_1, u_2, u_3, u_4)'$, then Equation 2 is transformed into the following normal form:

$$\frac{du_1}{dt} = -\sqrt{\frac{(1-\delta_1)\delta_1}{(1+\delta_1)\zeta}}\,u_2 + P(u_1, u_2, u_3, u_4),$$

$$\frac{du_2}{dt} = \sqrt{\frac{(1-\delta_1)\delta_1}{(1+\delta_1)\zeta}}\,u_1 + Q(u_1, u_2, u_3, u_4),$$

$$\frac{du_3}{dt} = -\frac{(\beta_2\delta_2+\delta_1(-1+\delta_2+\beta_2\delta_2))\varepsilon_1}{\beta_2+\delta_1+\beta_2\delta_1}u_3 + R(u_1, u_2, u_3, u_4),$$

$$\frac{du_4}{dt} = -\frac{(-1+(1+\beta_3(1+\delta_1)^2)\delta_3)\varepsilon_2}{1+\beta_3(1+\delta_1)^2}u_4 + S(u_1, u_2, u_3, u_4) \quad (4)$$

We obtained the quadratic and cubic items of P, Q, R and S, but they are too long to be displayed. Next, by the MATHEMATICA 7.0, we calculate the important quantities about P, all to be evaluated at $\beta_3 = \frac{1-\delta_1}{1+\delta_1}$,

$$g_{11} = i\frac{\sqrt{1-\delta_1}\sqrt{\delta_1}\sqrt{(1+\delta_1)\zeta}}{(\delta_1-1)\zeta^2},$$

$$g_{02} = \frac{1}{4}\left(-\frac{4i\sqrt{\delta_1}\sqrt{(1+\delta_1)\zeta}}{\sqrt{1-\delta_1}\,\zeta^2} + \frac{4\sqrt{\delta_1}(1+\delta_1)^2}{(1-\delta_1)^{3/2}\sqrt{(1+\delta_1)\zeta}} + \frac{4(1+\delta_1)}{(\delta_1-1)\zeta}\right),$$

$$g_{20} = \frac{1}{4}\left(-\frac{4i\sqrt{\delta_1}\sqrt{(1+\delta_1)\zeta}}{\sqrt{1-\delta_1}\,\zeta^2} + \frac{4\sqrt{\delta_1}(1+\delta_1)^2}{(1-\delta_1)^{3/2}\sqrt{(1+\delta_1)\zeta}} + \frac{4(1+\delta_1)}{(\delta_1-1)\zeta}\right),$$

$$G_{21} = \frac{1}{2}\left(\frac{3\delta_1(1+\delta_1)^3}{(\delta_1-1)^3\zeta} + i\frac{3\sqrt{(1-\delta_1)\delta_1}(1+\delta_1)^2\sqrt{(1+\delta_1)\zeta}}{(\delta_1-1)^3\zeta^2}\right).$$

We will find that there are not u_1^2, u_2^2 and u_1u_2 in the $R(u_1, u_2, u_3, u_4)$ and $S(u_1, u_2, u_3, u_4)$, we have

$$h^1_{11} = \frac{1}{4}\left(\frac{\partial^2 R}{\partial u_1^2} + \frac{\partial^2 R}{\partial u_2^2}\right) = 0,\quad h^2_{11} = \frac{1}{4}\left(\frac{\partial^2 S}{\partial u_1^2} + \frac{\partial^2 S}{\partial u_2^2}\right) = 0,$$

$$h^1_{20} = \frac{1}{4}\left(\frac{\partial^2 R}{\partial u_1^2} - \frac{\partial^2 R}{\partial u_2^2} - 2i\frac{\partial^2 R}{\partial u_1\partial u_2}\right) = 0,$$

$$h^2_{20} = \frac{1}{4}\left(\frac{\partial^2 S}{\partial u_1^2} - \frac{\partial^2 S}{\partial u_2^2} - 2i\frac{\partial^2 S}{\partial u_1\partial u_2}\right) = 0,$$

Solving the following equations

$$D\omega_{11} = -h_{11},\quad \left(D - 2i\sqrt{\frac{(1-\delta_1)\delta_1}{(1+\delta_1)\zeta}}\right)\omega_{20} = -h_{20},$$

Where

$$D = \begin{pmatrix}\lambda_3 & 0\\ 0 & \lambda_4\end{pmatrix},\quad h_{11} = \begin{pmatrix}h^1_{11}\\ h^2_{11}\end{pmatrix},\quad h_{20} = \begin{pmatrix}h^1_{20}\\ h^2_{20}\end{pmatrix},$$

one obtains $\omega_{11} = 0$, $\omega_{20} = 0$. Furthermore,

$$G^1_{110} = \frac{1}{2}\left[\frac{\partial^2 P}{\partial u_1\partial u_3} + \frac{\partial^2 Q}{\partial u_2\partial u_3} + i\left(\frac{\partial^2 Q}{\partial u_1\partial u_3} - \frac{\partial^2 P}{\partial u_2\partial u_3}\right)\right]$$

$$G^2_{110} = \frac{1}{2}\left[\frac{\partial^2 P}{\partial u_1\partial u_4} + \frac{\partial^2 Q}{\partial u_2\partial u_4} + i\left(\frac{\partial^2 Q}{\partial u_1\partial u_4} - \frac{\partial^2 P}{\partial u_2\partial u_4}\right)\right],$$

$$G^1_{101} = \frac{1}{2}\left[\frac{\partial^2 P}{\partial u_1\partial u_3} - \frac{\partial^2 Q}{\partial u_2\partial u_3} + i\left(\frac{\partial^2 Q}{\partial u_1\partial u_3} + \frac{\partial^2 P}{\partial u_2\partial u_3}\right)\right],$$

$$G^2_{101} = \frac{1}{2}\left[\frac{\partial^2 P}{\partial u_1\partial u_4} - \frac{\partial^2 Q}{\partial u_2\partial u_4} + i\left(\frac{\partial^2 Q}{\partial u_1\partial u_4} + \frac{\partial^2 P}{\partial u_2\partial u_4}\right)\right],$$

$$g_{21} = G_{21} + \left(2\sum_{k=1}^{2} G^k_{110}\,\omega^k_{11} + \sum_{k=1}^{2} G^k_{110}\,\omega^k_{20}\right).$$

In virtue of the above analysis, we can compute the following quantities

$$C_1(0) = \frac{i}{2\omega_0}\left(g_{20}g_{11} - 2|g_{11}|^2 - \frac{1}{3}|g_{02}|^2\right) + \frac{g_{21}}{2}$$

$$= \frac{1}{12(1-\delta_1)^3\sqrt{1-\delta\zeta}\,\zeta^{5/2}}\left((\delta_1+1)(9\sqrt{1-\delta\zeta_1}\,\zeta^{3/2}\delta_1^{7/2} + i\sqrt{1+\delta_1}(2\zeta^2 - 9\zeta + i6\zeta + 8)\delta_1^3\right.$$

$$+2\sqrt{(1-\delta_1)\zeta}(9\zeta - 2i\zeta + 3)\delta_1^{5/2} + 2i\sqrt{1+\delta_1}(2\zeta^2 - \zeta - 8)\delta_1^2 + (9-8)i\sqrt{1-\delta_1}\zeta^{3/2}\delta_1^{3/2}$$

$$\left.+\sqrt{1+\delta_1}(9i\zeta - 2i\zeta^2 + 6\zeta + 8)i\delta_1 - 4i\sqrt{(1-\delta_1)\delta}\zeta_1^{3/2} + 2i\zeta\sqrt{1+\delta_1} - 6\sqrt{(1-\delta_1)\zeta}\right),$$

$$\mu_2 = \frac{2\sqrt{\delta_1(\delta_1+1)}(\delta_1^2-1)\sqrt{\zeta}}{\sqrt{1-\delta_1}} - 3\delta_1(1+\delta_1)^2\zeta + 2(1-\delta_1^2),$$

$$\tau_2 = \frac{(\delta_1+1)^2}{12(1-\delta_1)^{9/2}\delta\zeta_1^2}\left(2\sqrt{1+\delta}\delta_1^{3/2}\zeta^{5/2}(8\delta_1 - 3\delta_1^2 - 3) + \sqrt{1-\delta_1}\delta^2(9\delta^2\zeta^2 + 2\zeta^2\delta - 3\zeta\delta\right.$$

$$\left.+8\delta_1 - 5\zeta^2 - 14\zeta - 16) - 4\sqrt{(\delta_1+1)\delta\zeta_1}^{3/2} + \sqrt{1-\delta}\delta_1(2\zeta^2 + 15\zeta + 8) + \sqrt{2}\sqrt{1-\delta\zeta_1}\right),$$

$$\beta_2 = -\frac{1}{2(1-\delta_1)^{7/2}\zeta^2}(\delta+1)^2\left(-2\sqrt{\delta+1}\delta^{3/2}\sqrt{\zeta} + 3\sqrt{1-\delta}\delta^2\zeta + \sqrt{1-\delta}\delta(3\zeta+2)\right.$$

$$\left.+2\sqrt{(1+\delta_1)\delta_1\zeta} - 2\sqrt{1-\delta_1}\right].$$

Therefore, one obtains $\mu_2 > 0$ when $\zeta \in (0, \zeta_0)$ while $\mu_2 < 0$ when $\zeta \in (\zeta_0, +\infty)$, in which $\zeta_0 = \frac{(\sqrt{7}-4)(\delta_1 - 1)}{9\delta_1(\delta_1+1)}$ is the unique and positive root of $\mu_2 = 0$. Moreover, $\alpha'(0) < 0$ and the signs of μ_2 and β_2 are the same. Based on the above discussion, we have the following conclusion.

Theorem 2

Let $\{(\beta_3, \delta_1, \delta_2, \delta_3) \mid \delta_1 < 1, \delta_2 < 1, \delta_3 > \frac{1-\delta_3}{\delta_3(1-\delta_1^2)\beta_1(1-\delta_1 - \delta_1\beta_1)}\}$, $\lambda_{3,4} < 0$. Then

(1) The Hopf bifurcation is non-degenerate and supercritical and the direction of bifurcation is $\beta_1 < \frac{1-\delta_1}{1+\delta_1}$ when $\zeta \in (0, \zeta_0)$, and the bifurcating periodic solutions are stable;

(2) The Hopf bifurcation is nondegenerate and subcritical and the direction of bifurcation is $\beta_1 > \frac{1-\delta_1}{1+\delta_1}$ when $\zeta \in (\zeta_0, +\infty)$, and the bifurcating periodic solutions are unstable;

(3) When $\mu_2 < 0$, and the period of bifurcating periodic solutions increases; when $\tau_2 > 0$, and the period of bifurcating periodic solutions decreases. Meanwhile, the period and characteristic exponent are

$$T = 2\pi\sqrt{\frac{(1+\delta_1)\zeta}{(1-\delta_1)\delta_1}}(1 + \tau_2\varepsilon^2 + O(\varepsilon^4)),$$

$$\beta = \beta_2\varepsilon^2 + O(\varepsilon^4)\ \beta = \beta_2\varepsilon^2 + O(\varepsilon^4).$$

Therefore, by choosing the appropriate bifurcation parameter β_1, it is proved that this Equation 2 has a Hopf bifurcation when β_1 exceeds the critical value $\frac{1-\delta_1}{1+\delta_1}$. This theoretical result is consistent with the numerical results by Bockelman et al. (2004).

CONCLUSION AND REMARKS

In this paper, the dynamic complexities of a basic food web of four species are studied analytically. With precise symbolic computation and a completely mathematical analysis, we have obtained the conditions that the periodic solutions from Hopf bifurcation are stable or unstable with Z and W going to extinction. Furthermore, the chaotic solutions from the Hopf bifurcation can cause the population to run a higher risk of extinction due to the unpredictability (Bockelman et al., 2004). Thus, how to control chaos in the epidemic model is very important, which needs further investigation.

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