Euro. Jnl of Applied Mathematics (2012), *vol.* 23, *pp.* 777–796.
doi:10.1017/S0956792512000265

Stability and Hopf bifurcation analysis for Nicholson's blowflies equation with non-local delay†

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(*Received 6 February 2012; revised 25 July 2012; accepted 26 July 2012; first published online 10 August 2012*)

We consider a diffusive Nicholson's blowflies equation with non-local delay and study the stability of the uniform steady states and the possible Hopf bifurcation. By using the upper- and lower solutions method, the global stability of constant steady states is obtained. We also discuss the local stability via analysis of the characteristic equation. Moreover, for a special kernel, the occurrence of Hopf bifurcation near the steady state solution and the stability of bifurcated periodic solutions are given via the centre manifold theory. Based on laboratory data and our theoretical results, we address the influence of various types of vaccinations in controlling the outbreak of blowflies.

Key words: Nicholson's blowflies equation; Diffusion; Non-local delay; Hopf bifurcation; Homogeneous Neumann boundary condition

1 Introduction

The Australian sheep blowfly (or *Lucilia cuprina*) is known as a worldwide pest of sheep. Usually, the Australian sheep blowfly lies in dead bodies and garbage tips. But if parts of the fleeces of sheep are contaminated with faeces and urine, the female *Lucilia cuprina* are attracted by the ammonia in urine and lie in those parts. The situation can be worse if the skin of sheep is irritated by urine, because the young larvae will grow and attack the living flesh of the sheep which causes the death of host sheep. From the early 1900s, the Australian sheep industry has been losing more than one hundred million dollars per annum [1, 3, 4] due to the flystrike of *Lucilia cuprina*. Recently, *Lucilia cuprina* has spread to Tasmania and New Zealand causing veterinary health problem and economic burden in all sheep rearing areas.

Over the years various methods of blowfly strike management have been tried and proved to be failure because of different reasons [3]. The traditional ones, such as the usage of chemical pesticides and radical surgery, are abandoned because of the

† Project supported in part by Natural Science and Engineering Research Council of Canada.

development of resistance to pesticides and opposition to surgical techniques based on ethical grounds. Recently, people began to advocate vaccination because of the possible potential of mimicking or enhancing the mechanisms of natural immunity. As we know, each technique has its own limitations and the effect can only be partial and transient. It is interesting to know how effective the strategy should be so that the *Lucilia cuprina* would extinct or the population keeps stable. From applied mathematical point of view, the establishment and discussion about the population model are then essential.

A pioneer study on the distribution of blowflies population was started by Nicholson [15], which concerned competition for food in laboratory fly populations. Based on Nicholson's data, Gurney *et al.* [10] posed a delay equation, which is now referred as the 'Nicholson's blowflies equation',

$$\frac{du}{dt} = -\delta u(t) + pu(t-\tau)\exp[-au(t-\tau)]. \tag{1.1}$$

Here p denotes the maximum per capita daily egg production rate, $1/a$ presents the size at which the blowfly population reproduces at its maximum rate, δ is the per capita daily adult death rate and τ is the generation time.

After Gurney *et al.*'s [10] work, some mathematicians have considered spacial influence on the spread of blowfly disease. So and Yang [18] studied the model

$$\frac{\partial \tilde{u}}{\partial t} = d\Delta\tilde{u}(t,x) - \tau\tilde{u}(t,x) + \beta\tau\tilde{u}(t-1,x)\exp[-\tilde{u}(t-1,x)], \tag{1.2}$$

the global stability of the equilibrium of equation (1.2) with the homogeneous Dirichlet boundary condition was given. The existence of Hopf bifurcation and its properties under the Neumann boundary condition was addressed in Yang and So [24].

Based on the model (1.2), distributed delay was introduced by Gourley and Ruan [7] in the following equation:

$$\frac{\partial u}{\partial t} = d\Delta u - \tau u(t,x) + \beta\tau\left(\int_{-\infty}^{t} f(t-s)u(s,x)ds\right)\exp\left(-\int_{-\infty}^{t} f(t-s)u(s,x)ds\right), \tag{1.3}$$

for $(x,t) \in \Omega \times [0,\infty)$, where Ω is either $\mathbb{R}^n$ or some finite domain, and the kernel function satisfies $f(t) \geqslant 0$ and

$$\int_0^\infty f(t)dt = 1, \quad \int_0^\infty tf(t)dt = 1. \tag{1.4}$$

In the work of Gourley and Ruan [7], the global and local stabilities of uniform steady states are studied. For the global stability, energy methods and a comparison principle for delay equation are employed.

It is getting to be noted that diffusion and time delays are not independent of each other and simply incorporating time delay into the reaction–diffusion system will bring some problems, since individuals may move around and are at different points at different times (see, e.g. [9, 22]). Britton [2] is the first to model delay and diffusion simultaneously for the Fisher equation on an infinite spatial domain, in which the so-called spatiotemporal delay or the non-local delay is introduced. As for the bounded domain, Gourley and

So [8] made some modifications in the model based on the work of Britton [2]. They showed that a spatial averaging kernel $G(x, y, t)$ should be involved in delayed terms, which is the fundamental solution of heat equation with proper initial data and boundary conditions. In particular, on the one-dimensional domain $[0, \pi]$, in the homogeneous Neumann problem,

$$G(x, y, t) = \frac{1}{\pi} + \frac{2}{\pi} \sum_{n=1}^{\infty} e^{-dn^2 t} \cos(nx) \cos(ny).$$

The problem of how the delay may be correctly incorporated into the equations has been receiving a great deal of attention, for more details we refer to [6, 9, 14, 19, 23].

In the present paper, we consider the following modified equation of equation (1.3) with non-local delay

$$\begin{aligned} \frac{\partial u(t,x)}{\partial t} &= d\Delta u(t,x) - \tau u(t,x) + \beta\tau (g * u)(t,x) \exp[-(g*u)(t,x)] \\ &= d\Delta u(t,x) - \tau u(t,x) + \beta\tau \int_{-\infty}^{t} \int_0^{\pi} G(x,y,t-s) f(t-s) u(s,y) dy ds \\ &\quad \times \exp[-\int_{-\infty}^{t} \int_0^{\pi} G(x,y,t-s) f(t-s) u(s,y) dy ds] \\ &=: d\Delta u(t,x) + Q(U_1, U_2) \end{aligned} \tag{1.5}$$

for $(t, x) \in [0, \infty) \times [0, \pi]$, with initial condition

$$u(s, x) = \phi(s, x) \geqslant 0, \ (s, x) \in (-\infty, 0] \times [0, \pi],$$

and the homogeneous Neumann boundary condition,

$$\frac{\partial u}{\partial x} = 0, \quad t > 0, \quad x = 0, \pi,$$

where $\phi \in C((-\infty, 0] \times [0, \pi])$ is the bounded, uniformly Hölder continuous, $\phi(0, x) \in C^1[0, \pi]$ and $U_1 = u(t, x), U_2 = (g * u)(t, x)$,

$$(g * u)(t, x) = \int_{-\infty}^{t} \int_0^{\pi} \left(\frac{1}{\pi} + \frac{2}{\pi} \sum_{n=1}^{\infty} e^{-dn^2(t-s)} \cos(nx) \cos(ny) \right) f(t-s) u(s, y) dy ds,$$

$f(t)$ satisfies equation (1.4) and it is easy to see that $\int_0^{\infty} \int_0^{\pi} G(x, y, s) f(s) dy ds = 1$.

As far as we know, the main topic discussed in most of the literature about equation (1.5) is the existence of travelling wave. For example, the existence of travelling wave-front solutions established in [13, 21] proved the existence of non-monotone travelling waves from the trivial solution to the positive equilibrium. Works about the dynamical behaviour around the uniform steady state solutions are few. In this paper, our main purpose is to investigate the stability of two constant steady states of equation (1.5) and possible Hopf bifurcation when the stability is lost. Moreover, as an application of our theoretical results, we will discuss the efficiency of different types of vaccinations based on some data collected under laboratory conditions.

This paper is organized as follows. In Section 2, the positivity and boundedness of solution to equation (1.5) are discussed. In Section 3, using the method of upper- and lower solutions and its associated monotone iteration scheme, we derived sufficient conditions for the global stability of constant steady states. It is noticeable that the energy methods used in [7] do not work for equation (1.5) because of spatial kernel. In Section 4, the local stability of steady state solutions is established via analysis of the corresponding characteristic equations. In Section 5, we discuss the occurrence of Hopf bifurcation when parameter τ passes critical values. The formula determining the stability of bifurcated periodic solutions on the centre manifold is given. In Section 6, numerical simulation results are shown to support our theoretical analysis. Conclusion and discussion are addressed in Section 7, where we apply theoretical results to analyse effects of various types of vaccinations. In this paper, for convenience, we always denote $\Omega = [0, \pi]$.

2 Positivity and boundedness of solution

In this section, we are concerned with the positivity and boundedness of solutions to equation (1.5). The positivity of solutions arising from population dynamics should be guaranteed because of biological realism. By using the strong maximum principle, via a similar process given in [7], we can have the positivity of solutions of equation (1.5). To prove the boundedness of solutions, we first introduce definition of sub- and super-solutions due to Redlinger [17], as it applies to our particular case.

Definition 2.1 *A pair of suitably smooth functions $v(t,x)$ and $w(t,x)$ is said to be a pair of sub- and super-solutions for equation (1.5), respectively, for $(t,x) \in [0,\infty) \times \Omega$ with the boundary condition $\nabla u \cdot n = 0$ on $\partial\Omega$ and initial condition $u(t,x) = \phi(t,x)$ for $t \leqslant 0$, $x \in \overline{\Omega}$, if the following conditions hold*

(i) $v(t,x) \leqslant w(t,x)$ for $(t,x) \in [0,\infty) \times \overline{\Omega}$.

(ii) The differential inequalities

$$\frac{\partial v(t,x)}{\partial t} \leqslant d\Delta v(t,x) - \tau v(t,x) + \beta\tau((g * \psi)(t,x)) \exp[-(g * \psi)(t,x)],$$

$$\frac{\partial w(t,x)}{\partial t} \geqslant d\Delta w(t,x) - \tau w(t,x) + \beta\tau((g * \psi)(t,x)) \exp[-(g * \psi)(t,x)]$$

hold for all functions $\psi \in C(([0,\infty) \times \overline{\Omega}) \cup ((-\infty,0] \times \overline{\Omega}))$, with $v \leqslant \psi \leqslant w$.

(iii) $\nabla v \cdot n = 0 = \nabla w \cdot n$ on $[0,\infty) \times \partial\Omega$.

(iv) $v(t,x) \leqslant \phi(t,x) \leqslant w(t,x)$ in $(-\infty,0] \times \overline{\Omega}$.

The following result is from Theorem 3.4 of [17], which shows the control of sub- and super-solutions on the solutions of equation (1.5).

Lemma 2.1 *Assume that $v(t,x)$ and $w(t,x)$ is a pair of sub- and super-solutions for equation (1.5). If $\phi \in C((-\infty,0] \times \overline{\Omega})$ is bounded, non-negative, uniformly Hölder continuous and $\phi_0(x) = \phi(0,x) \in C^1(\overline{\Omega})$, then there exists a unique regular solution $u(t,x)$ of the initial* *boundary value problem equation (1.5) such that*

$$v(t,x) \leqslant u(t,x) \leqslant w(t,x) \quad \textit{for} \quad (t,x) \in [0,\infty) \times \overline{\Omega}.$$

By the use of the above comparison lemma, we know that the positive solutions of equation (1.5) are bounded.

Lemma 2.2 *The solution* $u(t,x)$ *of equation (1.5) satisfies* $\lim_{t\to+\infty} \sup_{x\in\overline{\Omega}} u(t,x) \leqslant \frac{\beta}{e}$.

Proof. Let w_0 be the solution of the initial value problem $\frac{dw_0}{dt} = -\tau w_0 + \frac{\beta\tau}{e}, \quad t > 0$, with $w_0(0) = \sup_{s\in(-\infty,0]} \max_{x\in\Omega} \phi(s,x)$.

Define

$$\overline{w}_0(t) = \begin{cases} w_0(0), & t \in (-\infty, 0], \\ w_0(t), & t > 0. \end{cases}$$

Since $0 \leqslant \phi \leqslant w_0(0)$, we can choose $(0, \overline{w}_0)(t)$ as a pair of sub- and super-solutions of equation (1.5) under initial and boundary conditions. Actually, it is easy to see that 0 is a sub-solution. As for $\overline{w}_0$, since $ye^{-y} \leqslant e^{-1}$ for $y > 0$, one has

$$\begin{aligned} &\frac{\partial \overline{w}_0(t)}{\partial t} - d\Delta\overline{w}_0(t) + \tau\overline{w}_0(t) - \beta\tau((g * \psi)(t,x)) \exp[-(g * \psi)(t,x)] \\ &\geqslant \frac{\partial \overline{w}_0(t)}{\partial t} + \tau\overline{w}_0(t) - \frac{\beta\tau}{e} = 0 \end{aligned}$$

for any $\psi \in C(([0,\infty) \times \overline{\Omega}) \cup ((-\infty, 0] \times \overline{\Omega}))$, with $0 \leqslant \psi \leqslant \overline{w}_0$. This shows that $\overline{w}_0$ is a super-solution. Thus, Lemma 2.1 implies $0 \leqslant u(t,x) \leqslant \overline{w}_0$. Since $\lim_{t\longrightarrow\infty} \overline{w}_0(t) = \frac{\beta}{e}$, one has $\lim_{t\to+\infty} \sup_{x\in\overline{\Omega}} u(t,x) \leqslant \frac{\beta}{e}$. The proof is completed. □

3 Global asymptotic behaviour of uniform equilibria

It is readily seen that equation (1.5) admits a trivial steady-state solution and a non-trivial constant equilibrium $\ln\beta$ for $\beta > 1$. In this section, we study the global stability of the non-negative uniform steady-state solutions using the upper- and lower-solution methods developed by Pao [16].

To investigate the asymptotic dynamical behaviour, in the following we only need to consider equation (1.5) when $t \geqslant t_0$. According to Pao [16], if there exists $\widetilde{C} \geqslant \widehat{C} \geqslant 0$ such that

$$-\tau\widetilde{C} + \beta\tau\widetilde{C}e^{-\widetilde{C}} \leqslant 0 \leqslant -\tau\widehat{C} + \beta\tau\widehat{C}e^{-\widehat{C}}, \tag{3.1}$$

we call $\widetilde{C}$ and $\widehat{C}$ as upper- and lower-solutions for equation (1.5).

We can verify that $Q(U_1, U_2)$ defined in equation (1.5) satisfies the Lipschitz condition,

$$\begin{aligned} |Q(u_1,u_2) - Q(w_1,w_2)| &= | - \tau u_1 + \beta\tau u_2 e^{-u_2} - (-\tau w_1 + \beta\tau w_2 e^{-w_2})| \\ &\leqslant K(|u_1 - w_1| + |u_2 - w_2|) \end{aligned} \tag{3.2}$$

for all $\widehat{C} \leqslant u_i, w_i \leqslant \widetilde{C}, (i = 1, 2)$, where $K = K(\tau, \beta, \widetilde{C}, \widehat{C})$. Constructing two sequences

https://doi.org/10.1017/S0956792512000265 Published online by Cambridge University Press

$\{\overline{C}_m\}_{m=0}^{\infty}$ and $\{\underline{C}_m\}_{m=0}^{\infty}$ by the following iteration process

$$\begin{aligned}\overline{C}_m &= \overline{C}_{m-1} + \frac{1}{2K}(-\tau\overline{C}_{m-1} + \beta\tau\overline{C}_{m-1}e^{-\overline{C}_{m-1}}),\\ \underline{C}_m &= \underline{C}_{m-1} + \frac{1}{2K}(-\tau\underline{C}_{m-1} + \beta\tau\underline{C}_{m-1}e^{-\underline{C}_{m-1}}),\end{aligned} \tag{3.3}$$

with initial iteration $\overline{C}_0 = \widetilde{C}$ and $\underline{C}_0 = \widehat{C}$, respectively, condition (3.3) implies that

$$\widehat{C} \leqslant \underline{C}_m \leqslant \underline{C}_{m+1} \leqslant \overline{C}_{m+1} \leqslant \overline{C}_m \leqslant \widetilde{C}, m = 0, 1, 2 \dots. \tag{3.4}$$

Then the limits $\overline{\mathbf{C}} = \lim_{m\longrightarrow\infty}\overline{C}_m$, $\quad \underline{\mathbf{C}} = \lim_{m\longrightarrow\infty}\underline{C}_m$ exist and satisfy the equation

$$-\tau\overline{\mathbf{C}} + \beta\tau\overline{\mathbf{C}}e^{-\overline{\mathbf{C}}} = 0 = -\tau\underline{\mathbf{C}} + \beta\tau\underline{\mathbf{C}}e^{-\underline{\mathbf{C}}}. \tag{3.5}$$

Constants $\overline{\mathbf{C}}$ and $\underline{\mathbf{C}}$ are said to be quasi-solutions of equation (1.5) in the interval $[\widehat{C}, \widetilde{C}]$. In general, $\overline{\mathbf{C}}$ and $\underline{\mathbf{C}}$ are not the solution of equation (1.5). If $\overline{\mathbf{C}} = \underline{\mathbf{C}}$, it is a unique solution of equation (1.5) in the interval $[\widehat{C}, \widetilde{C}]$. The following result is a consequence of Theorems 2.1 and 2.2 of [16].

Theorem 3.1 *Assume that $\widetilde{C}$ and $\widehat{C}$ is a pair of upper- and lower solutions of equation (1.5). Then the sequences $\{\overline{C}_m\}_{m=0}^{\infty}$ and $\{\underline{C}_m\}_{m=0}^{\infty}$ defined by (3.3) converge monotonically to their respective limits $\overline{\mathbf{C}}$ and $\underline{\mathbf{C}}$ which, are the quasi-solution of equation (1.5) and satisfy (3.5). If $\overline{\mathbf{C}} = \underline{\mathbf{C}}$, then $\overline{\mathbf{C}}$ (or $\underline{\mathbf{C}}$) is a unique solution of equation (1.5) in the interval $[\widehat{C}, \widetilde{C}]$ for any initial function satisfying $\phi \in [\widehat{C}, \widetilde{C}]$ and the corresponding solution u of equation (1.5) satisfies $\lim_{t\longrightarrow\infty} u(t,x) = \overline{\mathbf{C}}$.*

Now we are in a position to state and prove our main results on the global stability of two-constant steady-state solutions, since the kernel function $f(x)$ satisfies the assumption in [16].

Theorem 3.2

(1) *If $1 < \beta \leqslant e$, $\ln\beta$ is globally stable, i.e. any non-trivial solution $u(t,x)$ of equation (1.5) with initial boundary conditions satisfies $\lim_{t\longrightarrow\infty} u(t,x) = \ln\beta$ uniformly in $x \in \Omega$.*

(2) *If $\beta < 1$, $u = 0$ is globally stable.*

Proof. (1) When $1 < \beta < e$, according to Lemma 2.2, for any $0 < \epsilon < 1 - \frac{\beta}{e}$, there exists t_0 such that $u(t,x) \leqslant \frac{\beta}{e} + \epsilon$ for $t > t_0$. Then $\widetilde{C} = \frac{\beta}{e} + \epsilon$, $\widehat{C} = \varepsilon_0$, $0 < \varepsilon_0 \leqslant \ln\beta$, as a pair of upper and lower solutions for equation (1.5). Note here $\ln\beta \leqslant \frac{\beta}{e} + \epsilon = \widetilde{C}$ since $\beta < e$. Then it is easy to see that inequality (3.1) holds for $1 < \beta < e$. Actually, since $1 < \beta < e$, we have $-1 + \beta e^{-(\frac{\beta}{e}+\epsilon)} \leqslant 0$, which means that $-\tau\widetilde{C} + \beta\tau\widetilde{C}e^{-\widetilde{C}} = \tau(\frac{\beta}{e} + \epsilon)(-1 + \beta e^{-(\frac{\beta}{e}+\epsilon)}) \leqslant 0$; and since $0 < \varepsilon_0 \leqslant \ln\beta$, $-1 + \beta e^{-\varepsilon_0} \geqslant 0$, i.e. $-\tau\widehat{C} + \beta\tau\widehat{C}e^{-\widehat{C}} = \varepsilon_0\tau(-1 + \beta e^{-\varepsilon_0}) \geqslant 0$.

By constructing the iteration process (3.3), we know (3.4) holds, so both of the limits of $\{\overline{C}_m\}_{m=0}^{\infty}$ and $\{\underline{C}_m\}_{m=0}^{\infty}$ exist and satisfy $0 < \overline{\mathbf{C}} \leqslant \frac{\beta}{e}$, $\quad 0 < \underline{\mathbf{C}} \leqslant \frac{\beta}{e}$. Furthermore, according

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to (3.5), we have

$$-1 + \beta e^{-\overline{\mathbf{C}}} = -1 + \beta e^{-\underline{\mathbf{C}}} = 0,$$

i.e. $\underline{\mathbf{C}} = \overline{\mathbf{C}} = \ln\beta$. Therefore, $\lim_{t\longrightarrow\infty} u(t,x) = \ln\beta$ uniformly in $x \in \Omega$, for $1 < \beta < e$.

When $\beta = e$, taking $\widetilde{C} = \widehat{C} = 1$ gives the result.

(2) For $\beta < 1$ we take $\widetilde{C} = \frac{\beta}{e}$ and $\widehat{C} = 0$ as a pair of upper and lower solutions. It is obvious that 0 is a lower solution. We only need to verify that $\tau\frac{\beta}{e}(\beta e^{-\frac{\beta}{e}} - 1) \leqslant 0$ holds, i.e. $\beta e^{-\frac{\beta}{e}} - 1 \leqslant 0$, which is obvious since $\frac{\beta}{e} \geqslant 0 \geqslant \ln\beta$. Thus, the limits $\overline{\mathbf{C}}$ and $\underline{\mathbf{C}}$ of the constructed iterative sequences satisfy $0 \leqslant \overline{\mathbf{C}} \leqslant \frac{\beta}{e}$, $\quad 0 \leqslant \underline{\mathbf{C}} \leqslant \frac{\beta}{e}$. From (3.5),

$$\underline{\mathbf{C}}\tau(-1 + \beta e^{-\underline{\mathbf{C}}}) = \overline{\mathbf{C}}\tau(-1 + \beta e^{-\overline{\mathbf{C}}}) = 0.$$

Since $\beta < 1$ and $\overline{\mathbf{C}}, \underline{\mathbf{C}} \geqslant 0$, we have $-1 + \beta e^{-\overline{\mathbf{C}}} < 0$, $-1 + \beta e^{-\underline{\mathbf{C}}} < 0$ and then $\underline{\mathbf{C}} = \overline{\mathbf{C}} = 0$. Therefore, $\lim_{t\longrightarrow\infty} u(t,x) = 0$ uniformly in $x \in \Omega$. □

4 Linearized stability of constant steady sate

In the previous section, we have proved that the trivial steady-state solution is globally stable for $0 < \beta < 1$, and the positive steady-state $u^* = \ln\beta$ is feasible when $\beta > 1$ and globally stable for $1 < \beta \leqslant e$. $\beta = 1$ is a critical value after which uniform steady state $\ln\beta$ appears and 0 begins to loose its stability. For $\beta > e$, we consider the local stability of $u^* = \ln\beta$. Let $u = \ln\beta + U$. The linearized system of equation (1.5) at $u^* = \ln\beta$ is

$$\frac{\partial U(t,x)}{\partial t} = d\Delta U(t,x) - \tau U(t,x) + \tau(1 - \ln\beta)(g * U)(t,x) =: L(\tau)U. \tag{4.1}$$

A suitable trial solution is $U = e^{\lambda t}\cos mx$, $m = 0, 1, 2, \ldots$ The effect of the non-local term upon such a trial solution is $g * (e^{\lambda t}\cos(mx)) = \overline{f}(\lambda + dm^2)e^{\lambda t}\cos(mx)$. Substituting the trial solution into equation (4.1) yields the eigenvalue equation

$$F(\lambda) := \lambda + dm^2 + \tau - \tau(1 - \ln\beta)\overline{f}(\lambda + dm^2) = 0, \tag{4.2}$$

where $\overline{f}(\lambda + dm^2) = \int_0^\infty f(s)e^{-(\lambda+dm^2)s}ds$.

Theorem 4.1 *If $e < \beta \leqslant e^2$, the steady state $u^* = \ln\beta$ of equation(1.5) on $[0,\infty) \times [0,\pi]$ with the Neumann boundary condition is linearly stable for any delay kernel.*

Proof. First, it is easy to see that zero is not an eigenvalue. Then, we only need to prove that all the roots λ of equation (4.2) are in the left half of the complex plane for any $m^2 \geqslant 0$. If it is false, then there exists a root λ_0 with $Re\lambda_0 \geqslant 0$ for some $m^2 \geqslant 0$. Since $|\overline{f}(\lambda_0 + dm^2)| < 1$, for $e < \beta \leqslant e^2$, one has

$$\tau \leqslant |\lambda_0 + dm^2 + \tau| = |\tau(1 - \ln\beta)\overline{f}(\lambda + dm^2)| < \tau.$$

This is a contradiction. □

For $\beta > e^2$, we cannot follow the same way to analyse the local stability of uniform steady-state solution $\ln\beta$ for general kernel since λ is mathematically involved in $\overline{f}(\lambda+dm^2)$.

However, by applying the theory of complex variables, we can obtain some further sufficient stability conditions.

It follows from a general result in the complex variable theory that the number of roots of eigenvalue equation (4.2), $F(\lambda)=0$, in the right half of the complex plane will be determined by

$$\lim_{R\longrightarrow\infty}\frac{1}{2\pi i}\int_{\gamma(R)}\frac{F'(\lambda)}{F(\lambda)}d\lambda,$$

with $\gamma(R)$ being the closed semicircular contour centred at the origin and contained in $\mathrm{Re}\lambda \geqslant 0$. We know that if $\mathrm{Re}\lambda > 0$, $\overline{f}(\lambda+dm^2)\leqslant 1$. A similar analysis as that in [12] yields

$$\lim_{R\longrightarrow\infty}\frac{1}{2\pi i}\int_{\gamma(R)}\frac{F'(\lambda)}{F(\lambda)}d\lambda=\frac{1}{2}-\frac{1}{\pi}\lim_{R\longrightarrow\infty}\arg F(iR), \tag{4.3}$$

i.e. the number of the roots of equation (4.2) is determined by $\frac{1}{2}-\frac{1}{\pi}\lim_{R\longrightarrow\infty}\arg F(iR)$. It is easy to see that

$$F(0)=\tau\left(1-\int_0^\infty e^{-sdm^2}f(s)ds\right)+\tau\ln\beta\int_0^\infty e^{-sdm^2}f(s)ds+dm^2>0$$

for $\beta>1$. Moreover, we know that $|\mathrm{Re}F(iR)|$ is bounded and independent of R, $\mathrm{Im}F(iR)$ grows linearly with R, where

$$\mathrm{Re}F(iR)=\tau-\tau(1-\ln\beta)\int_0^\infty f(t)e^{-tdm^2}\cos Rtdt+dm^2 \tag{4.4}$$

and

$$\mathrm{Im}F(iR)=R+\tau(1-\ln\beta)\int_0^\infty f(s)e^{-sdm^2}\sin Rsds. \tag{4.5}$$

Then the total change in $\arg F(iR)$ as R goes from zero to infinity would be the values $(1-4n)\pi/2$, $n=0,\pm1,\pm2,\ldots$. According to equation (4.3), $\ln\beta$ is locally stable if and only if $n=0$, i.e. $\lim_{R\to+\infty}\arg F(iR)=\frac{\pi}{2}$.

In the following, we give two conditions to assure that either $\mathrm{Re}F(iR)>0$ or $\mathrm{Im}F(iR)>0$. In both cases, the curve of $F(iR)$ always lies in the first quadrant of the complex plane and $\lim_{n\to+\infty}\arg F(iR)=\frac{\pi}{2}$.

Theorem 4.2 *Let $\beta>e^2$. Assume that the kernel $f(t)$ satisfies $f''(t)\geqslant 0$, $f(\infty)=0$ and $f'(\infty)=0$. Then the steady state $u^*=\ln\beta$ of equation (1.5) is linearly stable.*

Proof. We will prove $\mathrm{Re}F(iR)>0$ for all $R\geqslant 0$ here. Actually, according to the form of $\mathrm{Re}F(iR)$ in (4.4), this assertion holds since $e^{-tdm^2}>0$, $1-\ln\beta<0$ and

$$\int_0^\infty f(t)\cos Rtdt=\frac{1}{R^2}\int_0^\infty f''(t)(1-\cos Rt)dt\geqslant 0$$

under the given assumption by using integration by parts twice. This implies that $\arg F(iR)$ can only be $\frac{\pi}{2}$ as R goes from zero to infinity. Thus, there is no root of $F(\lambda) = 0$ in the right half complex plane, so $u^* = \ln\beta$ is linearly stable. □

Theorem 4.3 *If $\beta > e^2$ and $\tau < \frac{1}{\ln\beta - 1}$, then the steady state $u^* = \ln\beta$ of equation (1.5) is linearly stable.*

Proof. Under the given condition, we can prove $\mathrm{Im}F(iR) > 0$. Indeed, according to the form of $\mathrm{Im}F(iR)$ in (4.5), we have for $\tau < \frac{1}{\ln\beta - 1}$

$$\mathrm{Im}F(iR) \geqslant R - \tau(\ln\beta - 1)\left|\int_0^\infty f(s)e^{-sdm^2}\sin Rsds\right| \geqslant R - \tau(\ln\beta - 1)R > 0$$

since

$$\left|\int_0^\infty f(s)e^{-sdm^2}\sin Rsds\right| \leqslant \int_0^\infty f(s)e^{-sdm^2}|\sin Rs|ds \leqslant R\int_0^\infty se^{-sdm^2}f(s)ds \leqslant R.$$

Thus, $\arg F(iR)$ must be $\pi/2$ as R goes to ∞. Similar to Theorem 4.2, $u^* = \ln\beta$ is linearly stable. □

Remark 4.1 *From the above discussion, we have the following results about the stability of the two constant steady-state solutions zero and $\ln\beta$, with β as parameter:*

(1) If $0 < \beta < 1$, $u = 0$ is globally stable as stated in Theorem 3.2;

(2) if $1 \leqslant \beta$, $u = 0$ loses its local stability; when $1 < \beta \leqslant e$, $u^* = \ln\beta$ is globally asymptotically stable, see Theorem 3.2;

(3) when $e < \beta \leqslant e^2$, $u = \ln\beta$ is linearly stable for all kernels, shown in Theorem 4.1; when $\beta > e^2$, $u^* = \ln\beta$ is linearly stable if kernel satisfies conditions of Theorems 4.2, or the inequality about τ and β in Theorem 4.3 holds.

Remark 4.2 *It is easy to see that the weak kernel $f(t) = e^{-t}$ is a convex function and satisfies conditions in Theorem 4.2. Therefore, with the distributive delay function e^{-t}, $u^* = \ln\beta$ is always locally asymptotically stable. In other words, a weak kernel cannot destabilize the uniform state u^*.*

5 Hopf bifurcation from the non-zero uniform state with strong kernel

In the previous section, with the widely used kernel, weak kernel, the stability of constant steady states solution $\ln\beta$ of system equation (1.5) is obtained in Theorem 4.2. But as for another frequently considered kernel function, strong kernel, the discussion in Theorem 4.2 does not work. How is the stability of $u^* = \ln\beta$ with strong kernel for $\beta > e^2$? This is our target in this section.

With strong kernel $f(t) = 4te^{-2t}$ satisfying equation (1.4), whose Laplace transform is $\overline{f}(\sigma) = 1/(1+\sigma/2)^2$, according to equation (4.2) the characteristic equation about $u^* = \ln\beta$

is, for $m = 0, 1, \ldots$

$$2\left(1+\frac{\lambda+dm^2}{2}\right)^2\frac{\lambda+dm^2}{2}+\tau\left(1+\frac{\lambda+dm^2}{2}\right)^2-\tau(1-\ln\beta)=0. \tag{5.1}$$

First, it is easy to verify that 0 is not an eigenvalue.

To examine the existence of pure imaginary eigenvalue and simplify the notation, let $\lambda = 2i\omega$, $\omega \in \mathbb{R}$, $d = 2\tilde{d}$. Then (5.1) becomes

$$\omega^2 = 3\tilde{d}^2m^4+(4+\tau)\tilde{d}m^2+\tau+1, \quad \omega^2=\frac{2\tilde{d}^3m^6+(4+\tau)\tilde{d}^2m^4+2(\tau+1)\tilde{d}m^2+\tau\ln\beta}{6\tilde{d}m^2+4+\tau},$$

which implies that there exist two sequences of critical values of τ satisfying

$$(1+\tilde{d}m^2)\tau^2+[4(1+2\tilde{d}m^2)(1+\tilde{d}m^2)+1-\ln\beta]\tau+4(1+\tilde{d}m^2)(1+2\tilde{d}m^2)^2=0, \tag{5.2}$$

for $m = 0, 1, \ldots$. Since $4(1+\tilde{d}m^2)(1+2\tilde{d}m^2)^2 > 0$ and $\tau > 0$, equation (5.2) has positive roots for τ if and only if

$$\ln\beta \geqslant 1+8(1+2\tilde{d}m^2)(1+\tilde{d}m^2)=:\ln\beta_m \quad (m=0,1,\ldots)$$

with $\beta_0 < \beta_1 < \beta_2 < \ldots$.

Therefore, the characteristic equation (5.1) has pure imaginary eigenvalue only if $\beta \geqslant \beta_0$. Moreover, since 0 is not an eigenvalue, for $e^2 < \beta < \beta_0 = e^9$ the steady state $\ln\beta$ is stable. If $\beta_0 < \beta < \beta_1$, equation (5.2) has a pair of roots (denoted by τ_{100} and τ_{200}) when $m = 0$, but no such roots when $m > 0$. Then equation (5.1) has a pair of pure imaginary eigenvalues when τ is one of τ_{100} or τ_{200}. As β increases and passes another critical value β_1 and $\beta_1 < \beta < \beta_2$, the number of roots to equation (5.2) increases. Besides two roots denoted by τ_{110} and τ_{210} for $m = 0$, equation (5.2) has two more roots (τ_{111}, τ_{211}) for $m = 1$, and no more when $m \geqslant 2$. In this case, equation (5.1) has a pair of imaginary eigenvalues if τ is one of the four values. Generally, assume $\beta_n < \beta < \beta_{n+1}, (n = 0, 1, \ldots)$, then equation (5.2) has roots τ_{1nm}, τ_{2nm} with $0 < \tau_{1nm} < \tau_{2nm}$ for $m = 0, 1, \ldots n$. At each critical value τ_{jnm} $(j = 1, 2)$, characteristic equation (5.1) has a pair of pure imaginary eigenvalues $\lambda = \pm i\omega_{jnm}$ $(j = 1, 2)$. Differentiating equation (5.1) implicitly with respect to τ at τ_{jnm} and using $\omega_{jnm}^2 = 3\tilde{d}^2m^4 + (4+\tau)\tilde{d}m^2 + \tau + 1$, we have, for $j = 1, 2$

$$\lambda'(\tau_{jnm}) = -\frac{1}{2}\,\frac{-\omega_{jnm}^2+\tilde{d}^2m^4+2\tilde{d}m^2+\ln\beta+2i\omega_{jnm}(\tilde{d}m^2+1)}{-2\omega_{jnm}^2+i\omega_{jnm}(6\tilde{d}m^2+4+\tau_{jnm})},$$

then

$$\begin{aligned}
\mathrm{Re}\lambda'(\tau_{jnm}) &= \frac{-\omega_{jnm}^2+\tilde{d}^{\,2}m^4+2\tilde{d}m^2+\ln\beta-(\tilde{d}m^2+1)(6\tilde{d}m^2+4+\tau_{jnm})}{4\omega_{jnm}^2+(6\tilde{d}m^2+4+\tau_{jnm})^2}\\
&= -\frac{(\tilde{d}m^2+1)\tau_{jnm}^2+[4(2\tilde{d}m^2+1)(\tilde{d}m^2+1)+1-\ln\beta]\tau_{jnm}+(\tilde{d}m^2+1)\tau_{jnm}^2}{\tau_{jnm}[4\omega_{jnm}^2+(6\tilde{d}m^2+4+\tau_{jnm})^2]}\\
&= -(1+dm^2)\frac{\tau_{jnm}-\tau_{knm}}{4\omega_{jnm}^2+(6\tilde{d}m^2+4+\tau_{jnm})^2}\begin{cases}>0, & \text{if } j=1\\ <0, & \text{if } j=2\end{cases} \quad (k=2-j+1).
\end{aligned}$$

Therefore, the transversality condition holds and Hopf bifurcation occurs. Summarizing the above analysis, we have the following.

Theorem 5.1 *For equation (1.5) with strong kernel, the uniform steady state* $u^* = \ln\beta$ *is globally stable for* $1 < \beta \leqslant e$*; and it is locally stable when* $e < \beta < e^9$*; as* $\beta > e^9$*, series of Hopf bifurcation can occur at* $\tau = \tau_{jnm}$ $(j = 1, 2;\ n, m = 0, 1, \ldots)$.

In the following, by using the centre manifold method, we investigate the direction of Hopf bifurcation at the critical value τ_0 with pure imaginary eigenvalues $\pm i\omega_0$, and the stability of the bifurcated periodic solutions.

Let $\tau = \tau_0$ and $u = U + \ln\beta$, then equation (1.5) becomes

$$\frac{\partial U}{\partial t} = L(\tau_0)U + F(\tau_0, U), \tag{5.3}$$

where $L(\tau_0)$ is defined in equation (4.1) and

$$F(\tau_0, U) = -\tau_0(g*U)^2(t,x) + \frac{\tau_0}{2}(g*U)^3(t,x) + \frac{\tau_0}{2}\ln\beta(g*U)^2(t,x) - \frac{\tau_0}{3!}\ln\beta(g*U)^3(t,x) + o(|U|^3).$$

According to Hassard *et al.* [11], the stability of the bifurcating periodic solutions and the bifurcation direction is determined by sign(Re$c_1(\tau_0)$) and $\mu_2 = -\frac{\mathrm{Re}\, c_1(\tau_0)}{\mathrm{Re}\lambda'(\tau_0)}$ respectively, where

$$c_1(\tau_0) = \frac{i}{2\omega_0}\left(g_{20}g_{11} - 2|g_{11}|^2 - \frac{1}{3}|g_{02}|^2\right) + \frac{g_{21}}{2}.$$

More specifically, if $m \neq 0$, $\mathrm{Re}c_1(\tau_0) = \frac{1}{2}\mathrm{Re}g_{21}$; whereas if $m = 0$,

$$\mathrm{Re}c_1(\tau_0) = \mathrm{Re}\left\{\frac{i}{2\omega_0}\left(g_{20}g_{11} - 2|g_{11}|^2 - \frac{1}{3}|g_{02}|^2\right) + \frac{g_{21}}{2}\right\},$$

where g_{20}, g_{11}, g_{02} are 'explicitly' given in (7.2) and g_{21} is given in (7.13) for $m \neq 0$ and (7.13) for $m = 0$ in given in Appendix A. Here, 'explicitly' means that these values are expressed by the original parameters and functions.

6 Numerical simulations

In this section we present some numerical simulations to support the previous theoretical analysis. As an example, we consider equation (1.5) with $d = 1$ and choose the initial condition and the homogeneous Neumann boundary condition as following:

$$\begin{aligned}
\frac{\partial u(t,x)}{\partial t} &= \Delta u(t,x) - \tau u(t,x) + \beta\tau\int_{-\infty}^{t}\int_0^{\pi} G(x,y,t-s)f(t-s)u(s)dyds \\
&\quad \times \exp\left[-\int_{-\infty}^{t}\int_0^{\pi} G(x,y,t-s)f(t-s)u(s)dyds\right] \\
u(t,x) &= c\sin^2 x + \ln\beta - 1,\ (t,x) \in (-\infty, 0] \times [0,\pi], \\
\frac{\partial u}{\partial x} &= 0, \quad t > 0, \quad x = 0, \pi,
\end{aligned} \tag{6.1}$$

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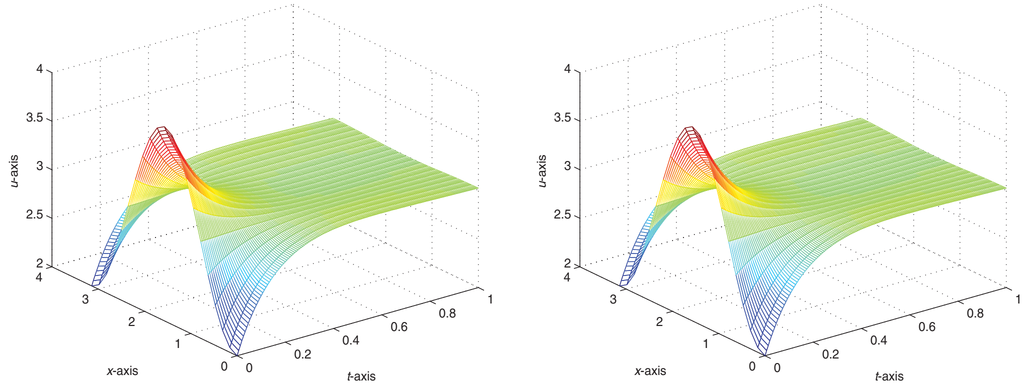

FIGURE 1. (Colour online) For $\beta = e^3$, $\tau = 1$ and $c = 2$, $u^* = \ln \beta = 3$ is stable. Left: weak kernel. Right: strong kernel.

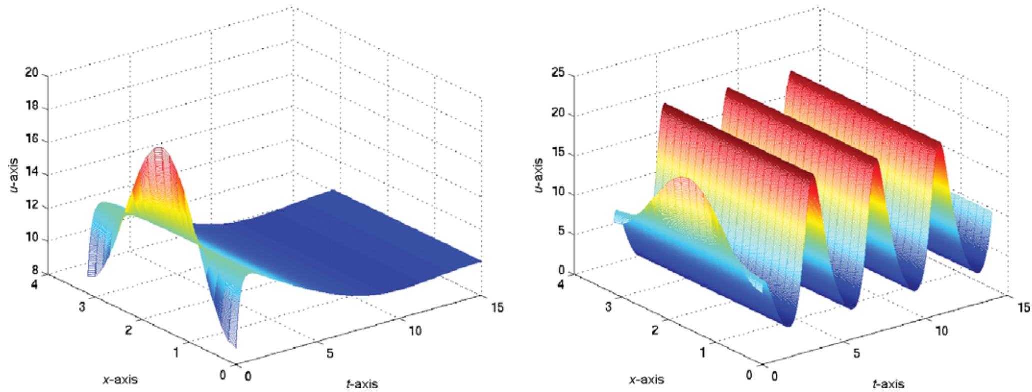

FIGURE 2. (Colour online) With $\beta = e^{10}$, strong kernel, $c = 10$. Left: $u^* = \ln \beta = 10$ is asymptotically stable when $\tau = \frac{1}{20} < \frac{1}{\ln \beta - 1}$. Right: positive solution converges to a periodic solution when $\tau = 1 > \frac{1}{\ln \beta - 1}$ and $\tau_{100} < \tau < \tau_{200}$.

where

$$G(x, y, t - s) = \frac{1}{\pi} + \frac{2}{\pi} \sum_{n=1}^{\infty} e^{-dn^2(t-s)} \cos(nx) \cos(ny)$$

and constant c is used to adjust the visibility of the numerical solution.

When $\beta > 1$, as shown in Theorem 4.2 and Section 5, u^* is stable for weak kernel, and when $1 < \beta < e^9$, strong kernel cannot destabilize the stability of u^*. To demonstrate the prediction, we choose $\beta = e^3$, $\tau = 1$ and $c = 2$. Then one can observe the stability of non-trivial equilibrium with both weak and strong kernels in Figure 1.

When $\beta > e^9$, if τ is small enough (i.e. $\tau < \frac{1}{\ln \beta - 1}$), the non-trivial steady-state u^* with strong kernel can keep its stability according to Theorem 4.3. By taking $\beta = e^{10}$, $c = 10$ and $\tau = \frac{1}{20} < \frac{1}{\ln \beta - 1}$, the left graph of Figure 2 demonstrates the stability of $u^* = 10$. Nevertheless, u^* may lose its stability as τ increases because of the occurrence of Hopf bifurcation from Theorem 5.1. Since $\beta_0 = e^9 < \beta = e^{10} < \beta_1 = e^{25}$, (5.2) has a pair of roots $\tau_{100} = \frac{1}{2}$ and $\tau_{200} = 2$ from which Hopf bifurcations occur and

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$\text{Re}\lambda'(\tau_{100}) > 0$, $\text{Re}\lambda'(\tau_{200}) < 0$. By using the explicit algorithm provided in the previous section for detecting the direction and stability of Hopf bifurcations, we have $\text{Re}c_1(\tau_{100}) \approx -1.3692 < 0$, i.e. from the critical value τ_{100} the bifurcated periodic solutions are stable and the Hopf bifurcation is supercritical. When choosing $\tau = 1 \in (\tau_{100}, \tau_{200})$, $c = 10$, there exists a positive solution that converges asymptotically to a periodic solution (see the right graph of Figure 2).

7 Conclusion and discussion

In this paper, we consider the diffusive Nicholson's blowflies model with non-local (or spatiotemporal) delay on a one-dimensional bounded domain. This spatial non-locality arises due to the fact that in biological models individuals usually have been at different points in spacial location at different times. We adopt the spatial averaging kernel introduced in [8], and by using the upper- and lower solution method, we have obtained sufficient conditions for the global convergence of uniform equilibrium to the proposed problem, which is determined by the value $\beta = \frac{p}{\delta}$. When the ratio β is less than one, the trivial equilibrium is proved to be globally stable, i.e. the population goes to extinction; and when this ratio is relatively small ($1 \leqslant \beta < e$), the population will be steady but small around the non-trivial steady-state solution $u^* = \ln\beta$.

Since the spatial averaging kernel is explicitly chosen, it enables us to analyse the local stability of uniform steady-state solutions by investigating the corresponding characteristic equations. We have proved that the non-trivial steady-state solution $u^* = \ln\beta$ is linearly stable when the ratio β is between e and e^2 for all kernels. When $\beta > e^2$, we have given conditions to assure the local stability of $u^* = \ln\beta$. Noting that the effect of a non-local term upon the characteristic equation is the appearance of $\overline{f}(\lambda + dm^2)$ instead of $\overline{f}(\lambda)$ in [7], since $|\overline{f}(\lambda + dm^2)| \leqslant |\overline{f}(\lambda)| < 1$ for $\text{Re}\lambda > 0$, we have similar results as that in [7] for local stability analysis.

Although the strong kernel $f(t) = 4te^{-2t}$ does not satisfy conditions in Theorem 4.2, if $\tau < \frac{1}{\ln\beta - 1}$, this kernel cannot destabilize the stability of non-trivial steady state $u^* = \ln\beta$ according to Theorem 4.3. When τ is relatively large, by investigating the distribution of eigenvalues, we found that there exist a series of $\beta_0 < \beta_1 < \ldots$ such that when $e < \beta < \beta_0 = e^9$, the local stability of the uniform steady-state solution $u^* = \ln\beta$ remains, when $\beta > \beta_0$, the strong kernel destabilizes the uniform steady-state $\ln\beta$ through Hopf bifurcations with τ as parameter. Moreover, when β passes $\beta_i, (i = 0, 1, \ldots)$, the number of critical values τ is $2(i + 1)$. Formulas determining direction of Hopf bifurcation and stability of bifurcated periodic solutions have been obtained by using centre manifold methods. Finally, numerical simulations are presented to demonstrate analytical results.

The non-locality can essentially affect dynamical properties. It is obvious that all the solutions approach to be spatially uniform in Figures 1 and 2, which is actually due to the fact that the non-locality is a form of spatial averaging and affects anything that is spatially heterogeneous [9]. In [6], a diffusive predator–prey system with non-local delay is studied. By considering various spatial and temporal kernels, some types of bifurcations can occur under the cooperation of diffusion and non-local delay, while such bifurcations cannot appear when the non-local delay degenerates into local delay. Such dynamical

Table 1. *Values for parameters in equation (1.1)*

	Description of parameter	Value
$1/a$	Population size at which the population achieves maximum reproductive success	$1/a \approx 450$
p	$\dfrac{\text{Maximum rate of egg-laying}}{\text{Population producing maximum reproduction}}$	$7.4 < p < 11.4$
δ	Per capita adult death rate	$0.17 < \delta < 0.23$
τ	Days that eggs take to develop into sexually matured adults	14.8 ± 0.4 days

behaviour is evidently not brought about by diffusion alone, but rather by the non-local delay in the system.

As introduced in [3], traditional methods of controlling flystrike are becoming less effective whereas vaccination against *Lucilia cuprina* has shown considerable potential. The study of the population dynamics of blowflies after sheep being vaccinated can help us appraise the potential of all the blowfly control measures listed above, on minimizing the incidence of flystrike in flocks. In the following, we will validate model (1.5) against the vaccination cases given in [3] and discuss the population dynamics corresponding to each vaccine according to our theoretical results. To do this, we need to evaluate the constant coefficients, especially the ratio β of the maximum per capita daily egg production rate p and the per capita daily adult death rate δ, and the time distribution kernel $f(t)$ in our mathematical model.

Note that there are some realistically feasible parameters in [10] which well explained Nicholson's data. We list values of some parameters for model (1.1) in Table 1. For more details about the calculation of these values, we refer to [10] and the references therein. But to analyse our cases, we need to do some modification about the estimation of p, the maximum per capita daily egg production rate. As we know, $R(u) = pu\exp(-au)$ in (1.1) describes the rate of recruitment to the adult population. In [10], p is simply the ratio of maximum rate of egg-laying and population producing maximum reproduction, which implies that the mortality rate of egg is ignored and all eggs mature into adults. This p is reasonable if the survival rate from egg to adult stage is very high. But considering the case that the sheep are vaccinated and the larval growth is greatly reduced, we modify p as $p' = p \times (1 - \text{reduction rate of larval growth})$. Then $\beta = p'/\delta$. By using the values of p and δ in Table 1, we can obtain the values of p' and β corresponding to each vaccination as shown in Table 2.

Zied *et al.* [25] collected the life-history raw data of *Lucilia cuprina* in laboratory conditions and obtained life tables of the sheep blowfly. According to their record, the probability that a newborn will survive to age x, which is also referred as the age-specific survival rate (l_x), shows weak distribution (Figure 2 in [25]). This suggests that the time distribution kernel $f(t) = e^{-t}$ in equation (1.5).

Based on the values of β listed in Table 2, we can receive some information about the population dynamics of blowflies. Note that for the first four vaccines $\beta > e^2$, according

Table 2. *Values of p' and β corresponding to each vaccination in [3]*

Vaccination	Reduction rate of larval growth	p'	$\beta = p'/\delta$
Detergent-insoluble fraction [4]	40% *in vivo*	$4.44 < p' < 6.84$	$19.30 < \beta < 40.24$
	50% *in vitro*	$3.70 < p' < 5.70$	$16.08 < \beta < 33.53$
Binding of MoAb to antigens [5]	33% *in vitro*	$4.96 < p' < 7.64$	$21.56 < \beta < 44.95$
PM [3]	30% *in vivo* and *in vitro*	$5.18 < p' < 7.98$	$22.52 < \beta < 46.94$
Glycoproteins [3]	50%	$3.70 < p' < 5.70$	$16.08 < \beta < 33.53$
Fourfold concentrationof immunoglobulin fraction from two of the antisera [3]	86%	$1.04 < p' < 1.60$	$4.52 < \beta \leqslant e^2$ $e^2 < \beta < 9.42$

Table 3. *Final population of Lucilia cuprina when the initial population is feasible*

Vaccination	$\ln \beta$	Final population of *Lucilia cuprina* $u^* = \ln \beta / a$
Detergent-insoluble fraction [4]	$2.9 < \ln \beta < 3.7$	(1,305, 1,665) *in vivo*
	$2.7 < \ln \beta < 3.6$	(1,215, 1,620) *in vitro*
Binding of MoAb to antigens [5]	$3.0 < \ln \beta < 3.9$	(1,350, 1,755) *in vitro*
PM [3]	$3.1 < \ln \beta < 3.9$	(1,395, 1,755) *in vivo* and *in vitro*
Glycoproteins [3]	$2.7 < \ln \beta < 3.6$	(1,215, 1,620)
Fourfold concentration of immunoglobulin fraction from two of the antisera [3]	$1.5 < \ln \beta < 2.0$	(675, 900)
	$2.0 < \ln \beta < 2.3$	(900, 1,035)

to Theorem 4.2 the non-trivial steady state $u^* = \ln \beta$ of equation (1.5) is locally stable. Recall that we did re-scaling from equations (1.1) to (1.5). Then with certain region of β, the final population will approach to u^*/a when the initial population is feasible, which is listed in Table 3. As for the last vaccine case when $e < \beta \leqslant e^2$, $u^* = \ln \beta$ is globally stable according to Theorem 4.1. This implies that the final population will be u^*/a irrespective of the initial population (see Table 3).

In summary, by applying our main theorem in Section 4, we can observe that all the vaccines in [3, 4, 5] would be expected to decrease the incidence and severity of blowfly strike on vaccinated sheep. Particularly, four-fold concentration of isolated immunoglobulin has shown considerable potential for controlling flystrike.

Appendix. Calculation of $g_{20}, g_{02}, g_{11}, g_{21}$

The eigenfunction corresponding to $i\omega_0$ is $\eta(\theta) = \cos(mx)e^{i\omega_0\theta}$ for $-\infty < \theta \leqslant 0$. The adjoint eigenfunction of $i\omega_0$ is $\eta^*(s) = De^{-i\omega_0 s}\cos(mx)$ for $0 \leqslant s < \infty$. Here $D = \frac{2}{\pi}[1-\tau_0(1-\ln\beta)\int_0^{+\infty} f(s)se^{i\omega_0 s}ds]^{-1}$ is obtained from $(\eta^*, \eta) = 1$ where the inner product is defined in [20]. The abstract form of (5.3) is

$$\frac{\partial U_t}{\partial t} = A_{\tau_0}U_t + \mathscr{X}_0 F(U_t), \tag{7.1}$$

where for $\phi \in C((-\infty, 0], X)$

$$A_{\tau_0}\phi(\theta) = \begin{cases} \frac{d\phi}{d\theta}, & -\infty < \theta < 0 \\ L(\phi), & \theta = 0 \end{cases} \quad \text{and} \quad \mathscr{X}_0 F(\phi)(\theta) = \begin{cases} 0, & -\infty < \theta < 0, \\ F(\phi), & \theta = 0 \end{cases}$$

with L, F defined in (5.3). Let $U_t = 2\mathrm{Re}\{\eta z\} + w$ with $z = (\eta^*, U_t)$. Then (7.1) becomes

$$\begin{aligned}
\frac{\partial z}{\partial t} &= i\omega_0 z + (\eta^*, \mathscr{X}_0 F(2\mathrm{Re}\{\eta z\} + w)) = i\omega_0 z + \Upsilon(z, \overline{z}, w), \\
\frac{\partial \overline{z}}{\partial t} &= -i\omega_0 \overline{z} + (\overline{\eta}^*, \mathscr{X}_0 F(2\mathrm{Re}\{\eta z\} + w)), \\
\frac{\partial w}{\partial t} &= A_{\tau_0} w + \mathscr{X}_0 F(2\mathrm{Re}\{\eta z\} + w) - 2\mathrm{Re}\{\eta(\eta^*, \mathscr{X}_0 F(2\mathrm{Re}\{\eta z\} + w))\} \\
&= A_{\tau_0} w + H(z, \overline{z}, w).
\end{aligned}$$

By using the expansion of $w(z,\overline{z}), \Upsilon(z,\overline{z}), H(z,\overline{z})$ and notations in [11], we can obtain $\Upsilon(z,\overline{z},w) = \frac{g_{20}}{2}z^2 + g_{11}z\overline{z} + \frac{g_{02}}{2}\overline{z}^2 + \frac{g_{21}}{2}z^2\overline{z} + \ldots$, where

$$g_{20} = \overline{g}_{02} = \begin{cases} 0, & m \neq 0, \\ 2\pi\tau_0 D\left(\frac{\ln\beta}{2} - 1\right)\overline{f}^2(i\omega_0), & m = 0, \end{cases} \qquad g_{11} = \begin{cases} 0, & m \neq 0, \\ 2\pi\tau_0 D\left(\frac{\ln\beta}{2} - 1\right)|\overline{f}(i\omega_0)|^2, & m = 0 \end{cases}$$

and

$$\begin{aligned}
g_{21} &= 4D\int_0^{\pi} \cos^{2(mx)} \tau_0(\frac{\ln\beta}{2} - 1)[\overline{f}(dm^2 + i\omega_0)(g * w_{11}) + \frac{1}{2}\overline{f}(dm^2 - i\omega_0)(g * w_{20})]dx + \\
&\quad \frac{9\pi\tau_0 D}{8}\left(1 - \frac{\ln\beta}{3}\right)\overline{f}\,(dm^2 + i\omega_0)\,|\overline{f}(dm^2 + i\omega_0)|^2.
\end{aligned} \tag{7.2}$$

Moreover, when $-\infty < \theta < 0$,

$$H(\theta, z, \overline{z}) = \begin{cases} O(|z|^3), & m \neq 0, \\ -\pi\tau_0(\overline{f}^2(i\omega_0)z^2 + \overline{f}^2(-i\omega_0)\overline{z}^2 + 2|\overline{f}(i\omega_0)|^2 z\overline{z}) & \\ \quad \times(e^{i\omega_0\theta}D + e^{-i\omega_0\theta}\overline{D})(\frac{\ln\beta}{2} - 1), & m = 0, \end{cases}$$

and when $\theta = 0$,

$$H(0, z, \overline{z}) = \begin{cases} \tau_0[\overline{f}^2(dm^2 + i\omega_0)z^2 + \overline{f}^2(dm^2 - i\omega_0)\overline{z}^2 + 2|\overline{f}^2(dm^2 + i\omega_0)|^2 z\overline{z}] & \\ \quad \times(\frac{\ln\beta}{2} - 1)\cos^2(mx), & m \neq 0, \\ \tau_0[\overline{f}^2(i\omega_0)z^2 + \overline{f}^2(-i\omega_0)\overline{z}^2 + 2|\overline{f}^2(i\omega_0)|^2 z\overline{z}] & \\ \quad \times(\frac{\ln\beta}{2} - 1)(1 - 2\pi\mathrm{Re}D), & m = 0. \end{cases}$$

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Then via a direct calculation, $H_{20} = \overline{H}_{02}$, when $-\infty < \theta < 0$

$$H_{20}(\theta) = \begin{cases} 0, & m \neq 0, \\ -2\pi\tau_0(e^{i\omega\theta}D + e^{-i\omega\theta}\overline{D})\left(\frac{\ln\beta}{2} - 1\right)\overline{f}^2(i\omega_0), & m = 0, \end{cases}$$

$$H_{11}(\theta) = \begin{cases} 0, & m \neq 0, \\ -2\pi\tau_0(e^{i\omega\theta}D + e^{-i\omega\theta}\overline{D})\left(\frac{\ln\beta}{2} - 1\right)|\overline{f}(i\omega_0)|^2, & m = 0, \end{cases}$$

and when $\theta = 0$

$$H_{20}(0) = \begin{cases} 2\tau_0\left(\frac{\ln\beta}{2} - 1\right)\cos^2(mx)\overline{f}^2(dm^2 + i\omega_0), & m \neq 0, \\ 2\tau_0\left(\frac{\ln\beta}{2} - 1\right)(1 - 2\pi\mathrm{Re}D)\overline{f}^2(i\omega_0), & m = 0, \end{cases}$$

$$H_{11}(0) = \begin{cases} 2\tau_0\left(\frac{\ln\beta}{2} - 1\right)\cos^2(mx)|\overline{f}(dm^2 + i\omega_0)|^2, & m \neq 0, \\ 2\tau_0\left(\frac{\ln\beta}{2} - 1\right)(1 - 2\pi\mathrm{Re}D)|\overline{f}(i\omega_0)|^2, & m = 0. \end{cases}$$

Since $H(\theta, z, \overline{z})$ is explicitly obtained, we are in a position to get $w_{20,}$ w_{11} and w_{02}. From [11], $w_{20} = \overline{w}_{02}$ and

$$[2i\omega_0 - A_{\tau_0}]w_{20}(\theta) = H_{20}(\theta), \quad -A_{\tau_0}w_{11}(\theta) = H_{11}(\theta). \tag{7.3}$$

Let $w_{20}(\theta) = A_1e^{-i\omega_0\theta} + A_2e^{i\omega_0\theta} + Ee^{2i\omega_0\theta}$. From (7.3), we have for $-\infty < \theta < 0$,

$$3i\omega_0A_1e^{-i\omega_0\theta} + i\omega_0A_2e^{i\omega_0\theta} = \begin{cases} 0, & m \neq 0, \\ -2\pi\tau_0(e^{i\omega_0\theta}D + e^{-i\omega_0\theta}\overline{D})\left(\frac{\ln\beta}{2} - 1\right)\overline{f}^2(i\omega_0), & m = 0. \end{cases}$$

Then

$$A_1 = \begin{cases} 0, & m \neq 0, \\ \frac{2\pi\tau_0\overline{D}i}{3\omega_0}\left(\frac{\ln\beta}{2} - 1\right)\overline{f}^2(i\omega_0), & m = 0, \end{cases} \quad A_2 = \begin{cases} 0, & m \neq 0, \\ \frac{2\pi\tau_0Di}{\omega_0}\left(\frac{\ln\beta}{2} - 1\right)\overline{f}^2(i\omega_0), & m = 0. \end{cases} \tag{7.4}$$

Since

$$\begin{aligned} &(2i\omega_0 - A_{\tau_0}(0))(Ee^{2i\omega_0\cdot}) \\ &= \begin{cases} 2\tau_0\left(\frac{\ln\beta}{2} - 1\right)\cos^2(mx)\overline{f}^2(dm^2 + i\omega_0), & m \neq 0, \\ 2\tau_0\left(\frac{\ln\beta}{2} - 1\right)\overline{f}^2(i\omega_0)[(1 - 2\pi\mathrm{Re}D) - (2i\omega_0 + \tau_0)\left(\frac{\overline{D}}{3} + D\right)\frac{\pi i}{\omega_0} & \\ \quad +(1 - \ln\beta)\left(\frac{\overline{D}}{3}\overline{f}(-i\omega_0) + D\overline{f}(i\omega_0)\right)\frac{\pi i}{\omega_0}], & m = 0, \end{cases} \end{aligned} \tag{7.5}$$

we are going to use the initial condition to determine E. When $m \neq 0$, let $E = E_1 + E_2\cos(2mx)$, $E_1, E_2 \in \mathbb{C}$, then from (7.5)

$$2i\omega_0E - d\Delta E + \tau_0E - \tau_0(1 - \ln\beta)(g * (Ee^{2i\omega_0\cdot})) = 2\tau_0\left(\frac{\ln\beta}{2} - 1\right)\frac{1 + \cos(2mx)}{2}\overline{f}^2(dm^2 + i\omega_0),$$

by solving the above equation, we have

$$E_1 = [2i\omega_0 + \tau_0 - \tau_0(1 - \ln\beta)\overline{f}(2i\omega_0)]^{-1}\tau_0\left(\frac{\ln\beta}{2} - 1\right)\overline{f}^2(dm^2 + i\omega_0),$$

$$E_2 = [2i\omega_0+4dm^2+\tau_0-\tau_0(1-\ln\beta)\overline{f}(4dm^2+2i\omega_0)]^{-1}\tau_0\left(\frac{\ln\beta}{2}-1\right)\overline{f}^2(dm^2+i\omega_0). \quad (7.6)$$

When $m=0$, letting $E=E_0\in\mathbb{C}$, via a direct calculation from (7.5), we have

$$E_0 = [2i\omega_0+\tau_0-\tau_0(1-\ln\beta)\overline{f}(2i\omega_0)]^{-1}2\tau_0\left(\frac{\ln\beta}{2}-1\right)\overline{f}^2(i\omega_0) \quad (7.7)$$
$$\times\left[(1-2\pi\mathrm{Re}D)-(2i\omega_0+\tau_0)\left(\frac{\overline{D}}{3}+D\right)\frac{\pi i}{\omega_0}+(1-\ln\beta)\left(\frac{\overline{D}}{3}\overline{f}(-i\omega_0)+D\overline{f}(i\omega_0)\right)\frac{\pi i}{\omega_0}\right].$$

Therefore, the explicit form of w_{20} is obtained and

$$(g*w_{20})=\begin{cases} A_1\overline{f}(-i\omega_0)+A_2\overline{f}(i\omega_0)+E_1\overline{f}(-2i\omega_0)+E_2\overline{f}(4dm^2+2i\omega_0)\cos(2mx), & m\neq 0,\\ E_0\overline{f}(-2i\omega_0), & m=0.\end{cases} \quad (7.8)$$

Similarly, let $w_{11}(\theta)=A_3e^{-i\omega_0\theta}+A_4e^{i\omega_0\theta}+M$, $A_3,A_4,M\in\mathbb{C}$. For $-\infty<\theta<0$,

$$-i\omega_0A_3e^{-i\omega_0\theta}+i\omega_0A_4e^{i\omega_0\theta}=-H_{11}(\theta).$$

It is a direct calculation to see that

$$A_3=\overline{A}_4=\begin{cases}0, & m\neq 0\\ -\dfrac{2\pi\tau_0\overline{D}i}{\omega_0}\left(\dfrac{\ln\beta}{2}-1\right)|\overline{f}(i\omega_0)|^2, & m=0.\end{cases}$$

For $\theta=0$, when $m\neq 0$, let $M=M_1+M_2\cos(2mx)$; when $m=0$, let $M=M_0$, we have

$$M_1 = \frac{1}{\ln\beta}\left(\frac{\ln\beta}{2}-1\right)|\overline{f}(dm^2+i\omega_0)|^2,$$
$$M_2 = -[\tau_0(1-\ln\beta)\overline{f}(4dm^2)-4m^2-\tau_0]^{-1}\tau_0\left(\frac{\ln\beta}{2}-1\right)|\overline{f}(dm^2+i\omega_0)|^2 \quad (7.9)$$

and

$$M_0=\frac{2\tau_0\left(\dfrac{\ln\beta}{2}-1\right)}{\ln\beta}|\overline{f}(i\omega_0)|^2[(1-2\pi\mathrm{Re}D)+\frac{2\pi\tau_0\overline{D}}{\omega_0}(\ln\beta-1)\mathrm{Im}\overline{f}(-i\omega_0)]. \quad (7.10)$$

Then w_{11} is well defined and

$$(g*w_{11})=\begin{cases}A_3\overline{f}(-i\omega_0)+A_4\overline{f}(i\omega_0)+M_1+M_2\overline{f}(4dm^2)\cos(2mx), & m\neq 0\\ M_0, & m=0.\end{cases} \quad (7.11)$$

Then by substituting w_{20},w_{11} into (7.2), we have for $m\neq 0$

$$g_{21}=2\pi\tau_0D\left(\frac{\ln\beta}{2}-1\right)\left[\frac{1}{2}\overline{f}(dm^2-i\omega_0)(A_1\overline{f}(-i\omega_0)+A_2\overline{f}(i\omega_0)+E_1\overline{f}(-2i\omega_0)\right. \quad (7.12)$$
$$\left.+\frac{1}{2}E_2\overline{f}(4dm^2+2i\omega_0))+\overline{f}(dm^2+i\omega_0)(2\mathrm{Re}\{A_3\overline{f}(-i\omega_0)\}+M_1)\right]$$
$$+\frac{9}{8}\pi\tau_0D\left(1-\frac{\ln\beta}{3}\right)\overline{f}(dm^2+i\omega_0)|\overline{f}(dm^2+i\omega_0)|^2$$

and for $m=0$

$$g_{21}=4\tau_0\pi D\left(\frac{\ln\beta}{2}-1\right)\left[\frac{1}{2}\overline{f}(-i\omega_0)E_0\overline{f}(-2i\omega_0)+\overline{f}(i\omega_0)M_0\right]+\frac{9}{8}\pi\tau_0D\left(1-\frac{\ln\beta}{3}\right)\overline{f}(i\omega_0)|\overline{f}(i\omega_0)|^2. \quad (7.13)$$

https://doi.org/10.1017/S0956792512000265 Published online by Cambridge University Press

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