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Global dynamics of Nicholson's blowflies equation revisited: Onset and termination of nonlinear oscillations

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ABSTRACT

We revisit Nicholson's blowflies model with natural death rate incorporated into the delay feedback. We consider the delay as a bifurcation parameter and examine the onset and termination of Hopf bifurcations of periodic solutions from a positive equilibrium. We show that the model has only a finite number of Hopf bifurcation values and we describe how branches of Hopf bifurcations are paired so the existence of periodic solutions with specific oscillation frequencies occurs only in bounded delay intervals. The bifurcation analysis and the Matlab package DDE-BIFTOOL developed by Engelborghs et al. guide some numerical simulations to identify ranges of parameters for coexisting multiple attractive periodic solutions.

1. Introduction

Experimental data collected by the Australian entomologist Nicholson [23,24] has motivated much entomological, mathematical and statistical research. In particular, Gurney et al. [10] proposed a delay differential equation to explain the oscillatory behavior of the observed sheep blowfly *Lucilia cuprina* population in [23]. The model developed by Gurney et al. [10] takes the simple-looking form

$$N'(t) = f\big(N(t-\tau)\big) - \gamma N(t) \tag{1.1}$$

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with $f(N) = pNe^{-\alpha N}$. Here $N(t)$ denotes the population of sexually mature adults at time t, p is the maximum possible per capita egg production rate, $1/\alpha$ is the population size at which the whole population reproduces at its maximum rate. In the model, τ is the generation time, or the time taken from eggs to sexually mature adults, and γ is the per capita mortality rate of adults. Model (1.1) is called Nicholson's blowflies equation. It was used by Oster and Ipaktchi [25] for the development of an insect population, and its modifications have been intensively studied in the literature of theoretical biology and delay differential equations. Notably, it has been shown that a unique positive equilibrium of (1.1) is globally asymptotically stable (with respect to nonnegative and nontrivial initial conditions) for any $\tau \geqslant 0$ provided that $1 < p/\gamma < e^2$ (see, for example, [12,16,28]). In the case where $p/\gamma > e^2$, the positive equilibrium loses its local stability and Hopf bifurcations occur at an unbounded sequence of critical values. The existence of periodic solutions when the delay τ is not necessarily near the local Hopf bifurcation values was established by Wei and Li [33], using a global Hopf bifurcation theorem coupled with Bendixson's criterion for higher dimensional ordinary differential equations.

In the aforementioned work and much of the existing literature, the mortality of the population during the maturation process has been ignored. Consideration of the survival probability during the maturation period requires an additional multiplier, which is delay-dependent, to be incorporated into the nonlinear delayed feedback term. This leads to the delay differential equation with a delay-dependent coefficient as follows:

$$N'(t) = e^{-\delta\tau} f\big(N(t-\tau)\big) - \gamma N(t), \tag{1.2}$$

where $\delta > 0$ is the death rate of the immature population. One can of course derive this model, as did in [3,22], from a structured population model for $u(t,a)$ (the population density at age a and time t) as below

$$\partial_t u(t,a) + \partial_a u(t,a) = -\mu(a) u(t,a),$$

with the stage-specific mortality rate

$$\mu(a) = \begin{cases} \gamma, & a > \tau, \\ \delta, & a < \tau. \end{cases}$$

A simple application of the integration along characteristic lines leads to the model equation for the matured population $N(t) = \int_\tau^\infty u(t,a)\,da$ with Ricker's type birth function f.

The additional term $e^{-\delta\tau}$ is the probability of immature population surviving τ time units before becoming mature. This addition, as we shall show, leads to rather different dynamics for model (1.2). More specifically, as the delay τ increases, the positive equilibrium loses its stability and undergoes local Hopf bifurcations at a *finite even number* of critical values, and as τ passes a critical threshold, the positive equilibrium regains its stability. As τ keeps increasing and passes another threshold value, the positive equilibrium disappears and the species becomes extinct (the zero solution is globally asymptotically stable). We also observe the coexistence of multiple stable periodic solutions. We note that the coexistence of stable periodic solutions has been a remarkable phenomena in biological systems [2,11,18,26] and our work seems to be the first result for the simple-looking blowflies delay differential equation.

The rest of this paper is organized as follows. Section 2 collects some preliminary results on the structure of equilibria, and the global stability of the trivial equilibrium. We then, in Section 3, focus on the (local) stability and Hopf bifurcation analysis about the positive equilibrium. The global continuation of Hopf bifurcations is examined in Section 4, and numerical simulations based on the bifurcation analysis are reported in Section 5. We then conclude the paper with a summary and some discussions in Section 6.