

DEPENDENCE OF STABILITY OF NICHOLSON'S BLOWFLIES EQUATION WITH MATURATION STAGE ON PARAMETERS*

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Abstract The stability of Nicholson's blowflies equation with maturation stage is investigated by reducing the number of parameters in the original model. We derive the condition on the stability of the positive equilibrium of the model, and discuss the dependence of the stability on the parameters by analyzing geometrically the dependence of real parts of eigenvalues of the characteristic equation with fewer parameters on the parameters. By restoring parameters, the condition on the stability of the positive equilibrium of the original model are formulated explicitly, and the corresponding regions are depicted for some different cases. The obtained result shows that the parameter determining the maximum reproductive success of the population affects only the size of the positive equilibrium, but plays no role in determining its stability.

Keywords Nicholson's blowflies equation, stability, maturation delay, parameters.

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1. Introduction

According to data drawn from the experiments on laboratory cultures of the sheep blowfly *Lucilia cuprina*, Nicholson [14] illustrated in 1953 the oscillatory population fluctuations by using the experimental and mathematical approaches, but the oscillatory behavior was not completely explained. In order to answer the associated questions, in 1980 Gurney et al. [7] formulated the Nicholson's blowflies equation

$$\frac{dN}{dt} = bN(t - \tau)e^{-\delta N(t - \tau)} - dN(t). \quad (1.1)$$

Here $N(t)$ denotes number of mature individuals at time t , the birth of new individuals is assumed to be subject to the Ricker function $be^{-\delta N}$ in which b is the maximum per capita production rate and $1/\delta$ is the population size at which the population as a whole achieves maximum reproductive success, d is the per capita death rate of mature population, and τ is the constant maturation time of new born individuals. The global attractivity, threshold dynamics and Hopf bifurcation of model (1.1) are further analyzed in [3, 8, 10–13, 16].

In model (1.1), the death of the immature population (i.e. in the maturation stage) is neglected. But the death in the stage is objective. Then when the death of

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the immature population is incorporated into (1.1) and the rate constant is assumed to be μ , Cooke et al. [5] derived the following delay differential equation

$$\frac{dN}{dt} = be^{-\mu\tau} N(t-\tau)e^{-\delta N(t-\tau)} - dN(t). \quad (1.2)$$

Model (1.2) has been applied to describe a predator-prey model with juvenile/mature class structure [4], the growth rate of adult female mosquitoes [6], and the change of total population in an SIS epidemic model with standard incidence in the absence of infection [5, 17, 18].

Dynamical behavior of equation (1.2) is complicated as the positive equilibrium exists, some results have been obtained by many mathematic researchers, but the analysis is far from complete. Shu et al. [15] considered the delay as a bifurcation parameter, examined the onset and termination of Hopf bifurcations of periodic solutions from the positive equilibrium, and showed that the model has only a finite number of Hopf bifurcation values and how branches of Hopf bifurcations are paired. In [19], the necessary and sufficient conditions ensuring the local stability of the positive equilibrium were found by applying the Pontryagin's method, and the effect of parameter values on the local stability of the equilibrium was investigated according to the obtained conditions. Cooke et al. [5] found the existence of stability switch of (1.2) (stable-unstable-stable) of the positive equilibrium as τ increases by using the geometric method. In [1, 9], the stability switches with increase of the delay were further investigated, and necessary and sufficient conditions of the local stability are provided by means of the geometric criterion proposed by Beretta and Kuang [2]. Wei and Zou [17] performed a global Hopf bifurcation analysis on (1.2) where b is used as a bifurcation parameter, and showed that model (1.2) actually allows multiple periodic solutions as b increases.

Although the unique difference between models (1.1) and (1.2) is only whether the death in the maturation stage is incorporated, the previous results show that, when both of them have a positive equilibrium, there are some essential discrepancies with respect to the existence and stability of the equilibrium. First, the equilibrium is $N^* = (1/\delta) \ln(b/d)$ for model (1.1) which needs $b > d$ [3, 9–12], and $N^* = [\ln(b/d) - \mu\tau]/\delta$ for model (1.2) which needs $be^{-\mu\tau} > d$ (i.e., $\tau < (1/\mu) \ln(b/d)$) [1, 5, 15, 17, 19]. The latter depends on the delay. Second, for model (1.1) the equilibrium is locally asymptotically stable as $d < b \leq be^2$ or $b > de^2$ and $\tau \in (0, \tau_0)$, and unstable as $b > de^2$ and $\tau > \tau_0$ [5, 12], where

$$\tau_0 = \frac{1}{d\sqrt{\ln \frac{b}{d} (\ln \frac{b}{d} - 1)}} \left[\pi - \arcsin \frac{\sqrt{\ln \frac{b}{d} (\ln \frac{b}{d} - 2)}}{\ln \frac{b}{d} - 1} \right];$$

for model (1.2) it is locally asymptotically stable as $d < be^{-\mu\tau} \leq de^2$ or $be^{-\mu\tau} > de^2$ and $[1 + \mu\tau - \ln(b/d)] \cos \omega_0 < 1$, and unstable as $be^{-\mu\tau} > de^2$ and $[1 + \mu\tau - \ln(b/d)] \cos \omega_0 > 1$ [19], where ω_0 is the root of equation $\tan \omega = -\omega/\tau$ in the interval $(\pi/2, \pi)$.

According to the conditions on the local stability of the equilibrium, it is easy to see that, for (1.1) it will no longer be stable once losing stability occurs when the delay increases. Note that ω_0 tends to $\pi/2$ as $\tau \rightarrow 0$, then, when the stability can change with increase of the delay, there must be stability switch for model (1.2), that is, after losing stability, its stability must restore and be preserved until the delay increases to $(1/\mu) \ln(b/d)$.

In this paper, our study is only concerned with the dependence of stability of the positive equilibrium $N^* = [\ln(b/d) - \mu\tau]/\delta$ of model (1.2) on all the parameters, so the corresponding discussion is only for the case $b > de^{\mu\tau}$. To this end, the associated analysis begins from the discussion on the characteristic equation of equation (1.2) at the equilibrium $N = N^*$. It is easy to know that the characteristic equation is

$$\lambda + d \left[1 - \left(1 + \mu\tau - \ln \frac{b}{d} \right) e^{-\lambda\tau} \right] = 0. \quad (1.3)$$

For simplicity, denoting $\bar{\lambda} = \lambda\tau$ and $\bar{\tau} = \mu\tau$, and then removing the bars, (1.3) reads the following equation

$$\lambda + \beta\tau [1 - (1 + \tau - \alpha)e^{-\lambda}] = 0, \quad (1.4)$$

where $\alpha = \ln(b/d)$ and $\beta = d/\mu$. Therefore, to discuss the stability of N^* is to determine whether the roots of equation (1.4) all have negative real parts for $\tau > 0$.

In the next section, we derive the other formulation of condition on the stability of equation (1.4), depict its stability region in the (α, β) -plane, and investigate the dependence of the region on delay. Finally, the obtained results in Section 2 are presented in terms of the original parameters in (1.3) (i.e. (1.2)), and the relations between two parameters of (1.2) ensuring the stability of the equilibrium are illustrated by some figures (Figures 4, 5 and 6).

2. Stability analysis of equation (1.4)

Since the stability change of (1.4) can occur only when its pure imaginary roots appear, we first consider the condition under which (1.4) has a pure imaginary root. Note that the left side of equation (1.4) is analytic with respect to ρ in the complex number field, thus substituting $\lambda = i\omega$ ($\omega > 0$) into (1.4) and separating the real and imaginary parts, we obtain

$$\begin{cases} 1 = (1 + \tau - \alpha) \cos \omega, \\ \omega = -\beta\tau(1 + \tau - \alpha) \sin \omega. \end{cases} \quad (2.1)$$

From (2.1) we have

$$\frac{\omega^2}{\beta^2\tau^2} + 1 = (1 + \tau - \alpha)^2.$$

That is,

$$\frac{\omega^2}{\beta^2\tau^2} = (2 + \tau - \alpha)(\tau - \alpha). \quad (2.2)$$

Since $\alpha > \tau$, from (2.2) it follows that (1.4) has no pure imaginary root as $\tau < \alpha < 2 + \tau$.

Furthermore, it is easy to see that there is no positive number ω satisfying (2.1) for the case $\alpha = 2 + \tau$. Therefore, we have

Proposition 2.1. The stability of (1.4) does not change for fixed τ as

$$(\beta, \alpha) \in D_1 := \{(\beta, \alpha) : \beta > 0, \tau < \alpha \leq 2 + \tau\}.$$

Obviously, when $\alpha > 2 + \tau$, the range of ω satisfying (2.1) is $\bigcup_{k=0}^{+\infty} I_k$, where $I_k = ((2k + \frac{1}{2})\pi, (2k + 1)\pi)$. Then, we obtain the equivalent form of (2.1)

$$\begin{cases} \alpha = 1 + \tau - \frac{1}{\cos \omega}, \\ \beta = -\frac{\omega}{\tau} \cot \omega, \end{cases} \tag{2.3}$$

where $\omega \in I_k (k = 0, 1, 2, \dots)$. Since

$$\frac{d\alpha}{d\omega} = -\frac{\sin \omega}{\cos^2 \omega} < 0, \quad \frac{d\beta}{d\omega} = \frac{\omega - \sin \omega \cos \omega}{\tau \sin^2 \omega} > 0,$$

then, when ω is regarded as a parameter, parametric equations (2.3) defines a series of functions $\alpha = \alpha_k(\beta) (k = 0, 1, 2, \dots)$, and for every function $\alpha = \alpha_k(\beta)$, $\frac{d\alpha}{d\beta} < 0$ for $\omega \in I_k$. Direct calculation gives

$$\frac{d^2\alpha}{d\beta^2} = -\frac{\tau^2 \sin^4 \omega [\omega(2 + \cos^2 \omega) - \sin \omega \cos \omega(3 + \sin^2 \omega)]}{\cos^3 \omega (\omega - \sin \omega \cos \omega)^3} > 0.$$

Then the curve corresponding to function $\alpha = \alpha_k(\beta)$ is decreasing and convex downwards.

Again, we have

$$\lim_{\omega \rightarrow (2k+1/2)\pi+0} \alpha = +\infty, \quad \lim_{\omega \rightarrow (2k+1/2)\pi+0} \beta = 0,$$

and

$$\lim_{\omega \rightarrow (2k+1)\pi-0} \alpha = 2 + \tau, \quad \lim_{\omega \rightarrow (2k+1)\pi-0} \beta = +\infty.$$

Then the straight lines $\beta = 0$ and $\alpha = 2 + \tau$ in the (β, α) plane are the asymptotes of the graph of function $\alpha = \alpha_k(\beta)$.

Further, according to the periodicity of cosine function and cotangent function, we know from (2.3) that the larger the subscript k is, the larger the value of β corresponding to the same α is. Therefore, if the curve corresponding to function $\alpha = \alpha_k(\beta)$ is denoted by L_k , any two curves L_m and L_n for $m > n (m, n = 0, 1, 2, \dots)$ do not intersect, and the curve L_m is always in the left lower of L_n (Fig. 1).

Since (2.1) and (2.3) are equivalent, for given τ equation (1.4) has pure imaginary roots if and only if the point (β, α) in the (β, α) plane is located on one of the curves $\{L_k\} (k = 0, 1, 2, \dots)$. Thus, we have the following statement.

Proposition 2.2. Equation (1.4) has no pure imaginary root for fixed τ as

$$(\beta, \alpha) \in D_2 := \{(\beta, \alpha) : \beta > 0, 2 + \tau < \alpha < \alpha_0(\beta)\}.$$

In order to find the region where all roots of equation (1.4) have negative real part, we have to determine the sign change of real part of root of (1.4) when point (β, α) crosses curves L_k . According to the properties of function $\alpha = \alpha_k(\beta)$, this can be carried out by considering the sign of the derivative of real part of the root with respect to β on L_k . So substituting $\rho = u + iv (v > 0)$ into (1.4) and separating the real and imaginary parts give

$$\begin{cases} F(u, v, \beta, \alpha) := u + \beta\tau - \beta\tau(1 + \tau - \alpha) \cos ve^{-u} = 0, \\ G(u, v, \beta, \alpha) := v + \beta\tau(1 + \tau - \alpha) \sin ve^{-u} = 0. \end{cases} \tag{2.4}$$

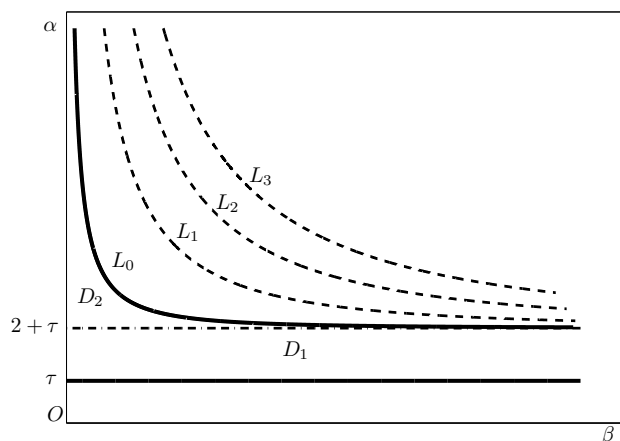


Figure 1. The graphs of functions $\alpha = \alpha_k(\beta)$ ($k = 0, 1, 2, \dots$) defined by parametric equations (2.3).

Obviously,

$$\begin{aligned} & \frac{\partial F}{\partial u} \cdot \frac{\partial G}{\partial v} - \frac{\partial F}{\partial v} \cdot \frac{\partial G}{\partial u} \\ &= [1 + \beta\tau(1 + \tau - \alpha) \cos ve^{-u}]^2 + [\beta\tau(1 + \tau - \alpha)e^{-u} \sin v]^2 > 0, \end{aligned}$$

then, according to the implicit function theorem, (2.4) only determines two functions $u = u(\beta)$ and $v = v(\beta)$. So from the implicit differentiation of $F(u, v, \beta, \alpha) = 0$ and $G(u, v, \beta, \alpha) = 0$ with respect to β , we have

$$\begin{cases} a \frac{\partial u}{\partial \beta} + b \frac{\partial v}{\partial \beta} = c_1, \\ -b \frac{\partial u}{\partial \beta} + a \frac{\partial v}{\partial \beta} = -c_2, \end{cases} \quad (2.5)$$

where

$$\begin{aligned} a &= 1 + \beta\tau(1 + \tau - \alpha) \cos ve^{-u}, & b &= \beta\tau(1 + \tau - \alpha)e^{-u} \sin v, \\ c_1 &= \tau [(1 + \tau - \alpha) \cos ve^{-u} - 1], & c_2 &= \tau(1 + \tau - \alpha) \sin ve^{-u}. \end{aligned}$$

From (2.5) it follows that

$$\frac{\partial u}{\partial \beta} = \frac{ac_1 + bc_2}{a^2 + b^2}.$$

Note that $u = 0$ and $v = \omega$ for $(\beta, \alpha) \in L_k$, then, applying (2.1) yields $a = 1 + \beta\tau$, $b = -\omega$, $c_1 = 0$ and $c_2 = -\frac{\omega}{\beta}$. Thus

$$\left. \frac{\partial u}{\partial \beta} \right|_{(\beta, \alpha) \in L_k} = \frac{\omega^2}{\beta [(1 + \beta\tau)^2 + \omega^2]} > 0.$$

It implies that the real part of root of equation (1.4) changes from negative to positive when the point (β, α) crosses curve L_k from left to right. Then, according

to the property of curves L_k , there must be a root of equation (1.4) with positive real part for $(\beta, \alpha) \in D' := \{(\beta, \alpha) : \beta > 0, \alpha > \alpha_0(\beta)\}$, that is, point (β, α) is above the curve L_0 . Therefore, we have the following result with respect to the instability of N^* .

Proposition 2.3. For fixed τ equation (1.4) has root with positive real part, that is, N^* is unstable, when point (β, α) is above the curve L_0 , i.e. $(\beta, \alpha) \in D' := \{(\beta, \alpha) : \beta > 0, \alpha > \alpha_0(\beta)\}$.

We claim that all roots of equation (1.4) have negative real part when

$$(\beta, \alpha) \in D_1 \cup D_2 = \{(\beta, \alpha) : \beta > 0, \tau < \alpha < \alpha_0(\beta)\} := D,$$

that is, the point (β, α) is between the straight line $\alpha = \tau$ and the curve L_0 . From the inferences above, (1.4) has no pure imaginary roots as $(\beta, \alpha) \in D$, then it is sufficient to prove that all roots of equation (1.4) have negative real part for the case $\alpha = 2 + \tau$.

When $\alpha = 2 + \tau$, (2.4) becomes

$$\begin{cases} u + \beta\tau + \beta\tau \cos ve^{-u} = 0, \\ v - \beta\tau \sin ve^{-u} = 0. \end{cases} \tag{2.6}$$

Obviously, for (2.6) we have $u = v = 0$ for $\beta = 0$. Further, from (2.6) it follows that $\frac{\partial u}{\partial \beta} \Big|_{\beta=0} = -2\tau < 0$. Then, $u < 0$ for $\beta > 0$ as $\alpha = 2 + \tau$. Thus the claim is true.

Summarizing the inference and discussion above, we have the following statements with respect to the stability of the positive equilibrium N^* .

Theorem 2.4. *The equilibrium $N = N^*$ is locally asymptotically stable when $(\beta, \alpha) \in D$ (i.e. $\tau < \alpha < \alpha_0(\beta)$), and unstable when $(\beta, \alpha) \in D'$ (i.e. $\alpha > \alpha_0(\beta)$).*

Theorem 2.4 implies that the graph of function $\alpha = \alpha_0(\beta)$ is a parameter separatrix determining whether (1.4) is stable for the fixed τ .

In the following, we consider the change of the region D with τ , that is, to discuss the relationship between two curves L_{01} and L_{02} corresponding to functions $\alpha = \alpha_{01}(\beta, \tau_1)$ and $\alpha = \alpha_{02}(\beta, \tau_2)$ with $\tau_1 > \tau_2 > 0$ respectively, which are defined respectively by the following parametric equations

$$\begin{cases} \alpha = 1 + \tau_1 - \frac{1}{\cos \omega}, \\ \beta = -\frac{\omega}{\tau_1} \cot \omega, \end{cases} \tag{2.7}$$

and

$$\begin{cases} \alpha = 1 + \tau_2 - \frac{1}{\cos \omega}, \\ \beta = -\frac{\omega}{\tau_2} \cot \omega, \end{cases} \tag{2.8}$$

where $\omega \in (\pi/2, \pi)$. For simplicity, we let $\sigma = \cos \omega$, then $\sigma \in (-1, 0)$ and $\omega = \arccos \sigma$. Correspondingly, parametric equations (2.7) and (2.8) become

$$\begin{cases} \alpha = 1 + \tau_1 - \frac{1}{\sigma_1} := \alpha(\sigma_1, \tau_1), \\ \beta = -\frac{\sigma_1 \arccos \sigma_1}{\tau_1 \sqrt{1 - \sigma_1^2}} := \beta(\sigma_1, \tau_1), \end{cases} \tag{2.9}$$

and

$$\begin{cases} \alpha = 1 + \tau_2 - \frac{1}{\sigma_2} := \alpha(\sigma_2, \tau_2), \\ \beta = -\frac{\sigma_2 \arccos \sigma_2}{\tau_2 \sqrt{1 - \sigma_2^2}} := \beta(\sigma_2, \tau_2), \end{cases} \quad (2.10)$$

respectively, where σ_1 and σ_2 ($\sigma_i \in (-1, 0)$, $i = 1, 2$) are parameters of parametric equations (2.9) and (2.10), respectively. To our end, we first discuss whether the curves L_{01} and L_{02} intersect.

The existence of their intersection point is equivalent to that of solution of the following equations

$$\begin{cases} \alpha(\sigma_1, \tau_1) = \alpha(\sigma_2, \tau_2), \\ \beta(\sigma_1, \tau_1) = \beta(\sigma_2, \tau_2). \end{cases}$$

From $\alpha(\sigma_1, \tau_1) = \alpha(\sigma_2, \tau_2)$ we have $\sigma_2 = \frac{\sigma_1}{1 + (\tau_2 - \tau_1)\sigma_1} := f_1(\sigma_1)$. For function $f_1(\sigma_1)$ with $\sigma_1 \in (-1, 0)$, direct calculation shows

$$f_1'(\sigma_1) = \frac{1}{[1 + (\tau_2 - \tau_1)\sigma_1]^2} > 0, \quad f_1''(\sigma_1) = \frac{2(\tau_1 - \tau_2)}{[1 + (\tau_2 - \tau_1)\sigma_1]^3} > 0,$$

and

$$f_1(0) = 0, \quad f_1'(-1) = 1, \quad f_1(-1) = -\frac{1}{1 + \tau_1 - \tau_2} > -1.$$

Therefore, the graph of function $\sigma_2 = f_1(\sigma_1)$ in $(-1, 0)$ is increasing and concave upward, and its range is $(-1/(1 + \tau_1 - \tau_2), 0)$ (Fig. 2).

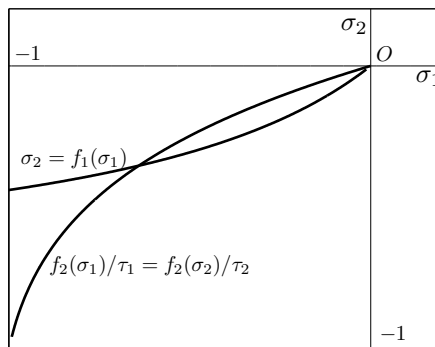


Figure 2. The curves of two implicit functions defined respectively by equations $\alpha(\sigma_1, \tau_1) = \alpha(\sigma_2, \tau_2)$ (i.e. $\sigma_2 = f_1(\sigma_1)$) and $\beta(\sigma_1, \tau_1) = \beta(\sigma_2, \tau_2)$ (i.e. $f_2(\sigma_1)/\tau_1 = f_2(\sigma_2)/\tau_2$).

On the other hand, from $\beta(\sigma_1, \tau_1) = \beta(\sigma_2, \tau_2)$ we have

$$\frac{f_2(\sigma_1)}{\tau_1} = \frac{f_2(\sigma_2)}{\tau_2}, \quad (2.11)$$

where $f_2(\sigma) = \frac{\sigma \arccos \sigma}{\sqrt{1 - \sigma^2}} < 0$.

For $\tau_1 > \tau_2$ and $f_2(\sigma_k) < 0$ ($k = 1, 2$) it follows from (2.11) that $f_2(\sigma_1) < f_2(\sigma_2)$. Then $\sigma_1 < \sigma_2$ since $f_2'(\sigma) = \frac{\arccos \sigma}{(1 - \sigma^2)^{3/2}} - \frac{\sigma}{1 - \sigma^2} > 0$ for $\sigma \in (-1, 0)$.

From (2.11) the implicit differentiation gives

$$\frac{d\sigma_2}{d\sigma_1} = \frac{\tau_2 f'_2(\sigma_1)}{\tau_1 f'_2(\sigma_2)} = \frac{g(\sigma_1)}{g(\sigma_2)} > 0, \tag{2.12}$$

where $g(\sigma) = \frac{f'_2(\sigma)}{f_2(\sigma)} < 0$. Further, from (2.12) we obtain

$$\begin{aligned} \frac{d^2\sigma_2}{d\sigma_1^2} &= \frac{1}{g^2(\sigma_2)} \left[g'(\sigma_1)g(\sigma_2) - g(\sigma_1)g'(\sigma_2) \frac{d\sigma_2}{d\sigma_1} \right] \\ &= \frac{g^2(\sigma_1)}{g(\sigma_2)} \left[\frac{g'(\sigma_1)}{g^2(\sigma_1)} - \frac{g'(\sigma_2)}{g^2(\sigma_2)} \right]. \end{aligned} \tag{2.13}$$

Denote $h(\sigma) = \frac{g'(\sigma)}{g^2(\sigma)}$, that is,

$$h(\sigma) = \frac{f''_2(\sigma)f_2(\sigma) - [f'_2(\sigma)]^2}{[f'_2(\sigma)]^2} = \frac{\sigma \arccos \sigma [3\sigma \arccos \sigma - \sqrt{1 - \sigma^2}(2 + \sigma^2)]}{(\arccos \sigma - \sigma\sqrt{1 - \sigma^2})^2} - 1,$$

then direct calculation yields

$$h'(\sigma) = \frac{\bar{h}(\sigma)}{(\arccos \sigma - \sigma\sqrt{1 - \sigma^2})^3},$$

where

$$\begin{aligned} \bar{h}(\sigma) &= \sigma \arccos \sigma [6(\arccos \sigma)^2 - 4 + 10\sigma^2] \\ &\quad - \left[\frac{2\sigma^4 + 2 - \sigma^2}{\sqrt{1 - \sigma^2}} (\arccos \sigma)^2 + \sigma^2(2 + \sigma^2\sqrt{1 - \sigma^2}) \right]. \end{aligned}$$

From $\arccos \sigma \in (\pi/2, \pi)$ for $\sigma \in (-1, 0)$ we know that $6(\arccos \sigma)^2 - 4 > 0$ for $\sigma \in (-1, 0)$. Then $h'(\sigma) < 0$ for $\sigma \in (-1, 0)$. Therefore, $h(\sigma_1) > h(\sigma_2)$ for $\sigma_1 < \sigma_2$. From (2.13) it follows that $\frac{d^2\sigma_2}{d\sigma_1^2} < 0$ for $\sigma_1 < \sigma_2$ since $g(\sigma) < 0$.

Again, from (2.11), that is,

$$\frac{\sigma_1 \arccos \sigma_1}{\tau_1 \sqrt{1 - \sigma_1^2}} = \frac{\sigma_2 \arccos \sigma_2}{\tau_2 \sqrt{1 - \sigma_2^2}},$$

we have $\lim_{\sigma_1 \rightarrow -1+0} \sigma_2 = -1$ and $\lim_{\sigma_1 \rightarrow 0-0} \sigma_2 = 0$. From $f'_2(0) = \frac{\pi}{2}$ it follows that $\left. \frac{d\sigma_2}{d\sigma_1} \right|_{\sigma_1=0} = \frac{\tau_2}{\tau_1} < 1$ for $\tau_1 > \tau_2$. Therefore, the graph of function defined by (2.11) is increasing and concave downward, and its range is $(-1, 0)$ (Fig. 2).

From the above inference, the curves of two implicit functions in the (σ_1, σ_2) plane defined respectively by equations $\alpha(\sigma_1, \tau_1) = \alpha(\sigma_2, \tau_2)$ and $\beta(\sigma_1, \tau_1) = \beta(\sigma_2, \tau_2)$ must intersect, and the intersection point is only one (Fig. 2).

Next, the horizontal asymptote $\alpha = 2 + \tau$ of function $\alpha = \alpha_0(\beta)$ moves up with increase of τ . Therefore, the curve of function $\alpha = \alpha_0(\beta)$ in the (β, α) moves upwards and leftwards with increase of τ (Fig. 3). Thus, the change of the region D with τ is clear.

3. Conclusion

In Section 2 we have found the parameter separatrix, $\alpha = \alpha_0(\beta)$, determining whether (1.4) is stable for the fixed τ . In order to directly determine whether the

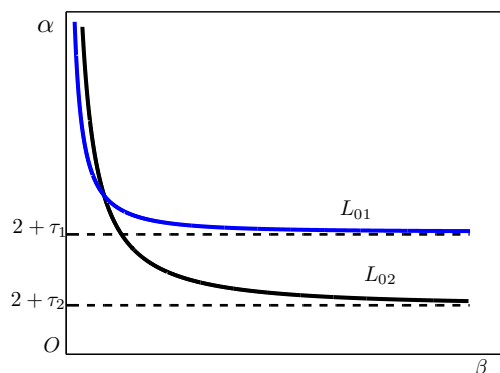


Figure 3. The graphs of functions $\alpha = \alpha_0(\beta)$ corresponding to different values of τ . Here, L_{0i} corresponds to τ_i ($k = 1, 2$) where $\tau_1 > \tau_2$.

equilibrium is stable in terms of the original parameters in model (1.2), it is required to express $\alpha = \alpha_0(\beta)$ with the parameters in model (1.2). To this end, according to transformation from (1.3) to (1.4), replacing τ, α and β in equations (2.3) with $\mu\tau, \ln(b/d)$ and d/μ , respectively, yields

$$\begin{cases} \ln \frac{b}{d} = 1 + \mu\tau - \frac{1}{\cos \omega}, \\ d = -\frac{\omega}{\tau} \cot \omega, \end{cases} \quad \omega \in \left(\frac{\pi}{2}, \pi\right). \quad (3.1)$$

Equation (3.1) can also be rewritten as

$$\begin{cases} b = -\frac{\omega \cot \omega}{\tau} \exp\left(1 + \mu\tau - \frac{1}{\cos \omega}\right), \\ d = -\frac{\omega}{\tau} \cot \omega, \end{cases} \quad \omega \in \left(\frac{\pi}{2}, \pi\right). \quad (3.2)$$

Then, for fixed μ and τ , equations (3.2) with parameter ω defines a function $b = b_0(d)$. Corresponding to function $\alpha = \alpha_0(\beta)$, function $b = b_0(d)$ determines whether the equilibrium of model (1.2) is stable. Similarly, the parametric equations (3.1) or (3.2) may also define function $\mu = \mu_0(d)$ for given b and τ , and function $b = b_1(\mu)$ for given d and τ . Their graphs are depicted in Figures 4, 5 and 6, respectively.

On the other hand, the condition on the existence of the positive equilibrium is $b > de^{\mu\tau}$, then, according to Theorem 2.4, we have the following statements with respect to stability of the positive equilibrium of model (1.2).

Theorem 3.1. *For fixed μ and τ , the positive equilibrium of model (1.2) is locally asymptotically stable as $de^{\mu\tau} < b < b_0(d)$, and unstable as $b > b_0(d)$.*

For fixed b and τ , the positive equilibrium of model (1.2) is locally asymptotically stable as $\mu_0(d) < \mu < (1/\tau) \ln(b/d)$, and unstable as $\mu > \mu_0(d)$.

For fixed d and τ , the positive equilibrium of model (1.2) is locally asymptotically stable as $de^{\mu\tau} < b < b_1(\mu)$, and unstable as $b > b_1(\mu)$.

According to Theorem 3.1, the stability regions of model (1.2) for the different cases are showed in Figures 4, 5 and 6, respectively. And the change of the regions with τ is also reflected in the corresponding figures.

At last, it must be pointed out that, with respect to dynamical behavior of model (1.2), the parameter δ determines only the value of the positive equilibrium, but does not affect its stability.

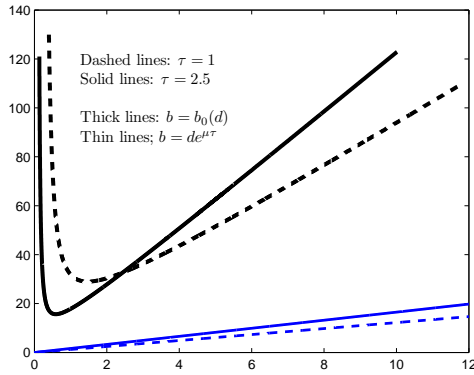


Figure 4. The stability regions of the positive equilibrium of (1.2) with different τ for $\mu = 0.2$. The equilibrium is locally asymptotically stable as point (d, b) is located in the region between two solid (or dashed) lines.

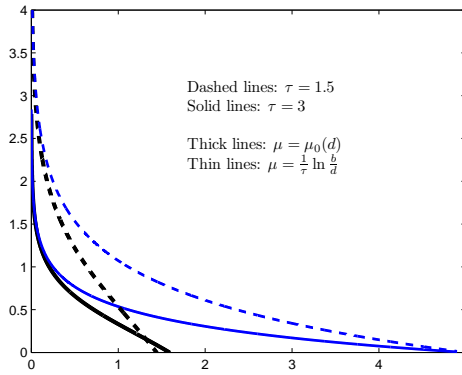


Figure 5. The stability regions of the positive equilibrium of (1.2) with different τ for $b = 5$. The equilibrium is locally asymptotically stable as point (d, b) is located in the region between two solid (or dashed) lines.

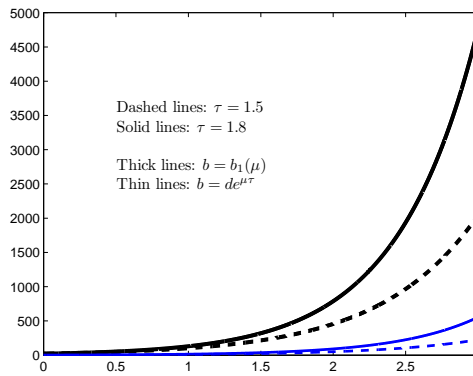


Figure 6. The stability regions of the positive equilibrium of (1.2) with different τ for $d = 2.5$. The equilibrium is locally asymptotically stable as point (d, b) is located in the region between two solid (or dashed) lines.

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References

[1] E. Beretta and D. Breda, *Discrete or distributed delay: Effects on stability of population growth*, Math. Biosci. Eng., 2016, 13(1), 19–41.

- [2] E. Beretta and Y. Kuang, *Geometric stability switch criteria in delay differential systems with delay dependent parameters*, SIAM J. Math. Anal., 2002, 33(5), 1144–1165.
- [3] L. Berezensky, E. Braverman and L. Idels, *Nicholson's blowflies differential equations revisited: Main results and open problems*, Appl. Math. Model., 2010, 34(6), 1405–1417.
- [4] K. L. Cooke, R. H. Elderkin and W. Huang, *Predator-prey interactions with delays due to juvenile maturation*, SIAM J. Appl. Math., 2006, 66(3), 1050–1079.
- [5] K. Cooke, P. van den Driessche and X. Zou, *Interaction of maturation delay and nonlinear birth in population and epidemic models*, J. Math. Biol., 1994, 99(4), 332–352.
- [6] G. Fan, J. Liu, P. van den Driessche, J. Wu and H. Zhu, *The impact of maturation delay of mosquitoes on the transmission of West Nile virus*, Math. Biosci., 2010, 228(2), 119–126.
- [7] M.S. Gurney, S. P. Blythe and R. M. Nisbet, *Nicholson's blowflies revisited*, Nature, 1980, 287(5777), 17–21.
- [8] I. Györi and S. Trofimchuk, *Global attractivity in $x'(t) = dx(t) + pf(x(t - \tau))$* , Dynam. Systems Appl., 1999, 8(2), 197–210.
- [9] Z. Jiang and W. Zhang, *Bifurcation analysis in single-species population model with delay*, Sci. China Math., 2010, 53(6), 1475–1481.
- [10] M. Kulenovic, G. Ladas and Y. Sficas, *Global attractivity in Nicholson's blowflies*, Appl. Anal., 1992, 43(5), 109–124.
- [11] J. Li, *Global attractivity in Nicholson's blowflies*, Appl. Math., 1996, 11B(4), 425–436.
- [12] M. Y. Li and J. Wei, *Hopf bifurcation analysis in a delayed Nicholson blowflies equation*, Nonlinear Anal., 2005, 60(7), 1351–1367.
- [13] E. Liz, V. Tkachenko and S. Trofimchuk, *A global stability criterion for scalar functional differential equations*, SIAM J. Math. Anal., 2003, 35(3), 596–622.
- [14] A.J. Nicholson, *An outline of the dynamics of animal populations*, Aust. J. Zool., 1954, 2(1), 9–65.
- [15] H. Shu, L. Wang and J. Wu, *Global dynamics of Nicholson's blowflies equation revisited: Onset and termination of nonlinear oscillations*, J. Differential equations, 3013, 255(9), 2565–2586.
- [16] H.L. Smith, *Monotone Dynamical Systems. An Introduction to the Theory of Competitive and Cooperative Systems*, AMS, Providence, RI, 1995.
- [17] J. Wei and X. Zou, *Bifurcation analysis of a population model and the resulting SIS epidemic model with delay*, J. Comput. Appl. Math., 2006, 197(1), 169–187.
- [18] X.-Q. Zhao and X. Zou, *Threshold dynamics in a delayed SIS epidemic model*, J. Math. Anal. Appl., 2001, 257(2), 282–291.
- [19] C. Zheng, F. Zhang and Jianquan Li, *Stability analysis of a population model with maturation delay and Ricker birth function*, Abstract and Applied Analysis, 2014, 2014(3), 1–8.