DISCRETE AND CONTINUOUS DYNAMICAL SYSTEMS Volume 9, Number 6, November 2003

pp. 1465 - 1492

HETEROCLINIC FOLIATION, GLOBAL OSCILLATIONS FOR THE NICHOLSON-BAILEY MODEL AND DELAY OF STABILITY LOSS

SZE-BI HSU

Department of Mathematics, National Tsing Hua University Hsinchu 300, TAIWAN

Ming-Chia Li

Department of Mathematics, National Changhua University of Education Changhua 500, TAIWAN

Weishi Liu

Department of Mathematics, University of Kansas Lawrence, Kansas 66045, USA

MIKHAIL MALKIN

Department of Mathematics, Nizhny Novgorod State University Nizhny Novgorod, RUSSIA

(Communicated by Jianhong Wu)

Abstract. This paper is concerned with the classical Nicholson-Bailey model [15] defined by $f_{\lambda}(x, y) = (y(1 - e^{-x}), \lambda y e^{-x})$. We show that for $\lambda = 1$ a heteroclinic foliation exists and for $\lambda > 1$ global strict oscillations take place. The important phenomenon of delay of stability loss is established for a general class of discrete dynamical systems, and it is applied to the study of nonexistence of periodic orbits for the Nicholson-Bailey model.

1. Introduction. Consider a system of difference equations of the form

$$x_{n+1} = cy_n(1 - g(x_n, y_n)), y_{n+1} = \lambda y_n g(x_n, y_n),$$

where $x_n, y_n \ge 0, n \in \mathbb{N}$, the numbers $c, \lambda > 0$ are parameters, and g is a continuous function with range in [0, 1]. A system of such a type is used as a host-parasite model [5], in which case x_n and y_n are the densities in the *n*th generation of parasites and hosts respectively, $g(x_n, y_n)$ is the fraction of hosts not parasitized, λ is the host reproductive rate, and c is the average number of viable eggs laid by a parasite on a single host. In 1935, Nicholson and Bailey [15] made assumptions on random encounters of hosts by parasites and on the rate of parasitism of a host, and under

¹⁹⁹¹ Mathematics Subject Classification. 37E30, 39A11, 92D25.

Key words and phrases. Nicholson-Bailey model, heteroclinic foliation, global oscillation, delay of stability loss, singular perturbation.

S.-B. Hsu, M.-C. Li, W. Liu and M. Malkin were partially supported by NSC grant 91-2115-M-007-012, NSC grant 91-2115-M-018-002, NSF grant DMS-0071931, and RFBR grant 02-01-000-98, respectively. M. Malkin is grateful to National Center for Theoretical Sciences in Taiwan for hospitality during his visit.

those assumptions the Poisson distribution for the densities leads to the following expression for the function g (see [5]):

$$g(x_n, y_n) = e^{-ax_n}$$

where a is a constant which represents the parasite searching efficiency. So the *Nicholson-Bailey model* is the system

$$x_{n+1} = cy_n(1 - e^{-ax_n}),$$

$$y_{n+1} = \lambda y_n e^{-ax_n}.$$

By the scaling $x \mapsto ax$, $y \mapsto cay$, the Nicholson-Bailey model takes the form

$$x_{n+1} = y_n (1 - e^{-x_n}),$$

$$y_{n+1} = \lambda y_n e^{-x_n}.$$
(1.1)

For any $\lambda > 0$ the Nicholson-Bailey map (1.1) is a diffeomorphism in the first quadrant of the (x, y)-plane (without the x-axis) onto itself. In the case when $0 < \lambda < 1$, the dynamics of the Nicholson-Bailey model is very simple (see Section 2): for every initial point from the open first quadrant Q, the forward orbit approaches exponentially the origin, while the backward orbit tends exponentially to infinity approaching the y-axis.

The case $\lambda = 1$ is a bifurcational one: in this case the y-axis consists of nonhyperbolic fixed points, and we are able to give an explicit expressions for the global stable and unstable manifolds of these fixed points (Theorem 3.1). In fact, we show that in the case when $\lambda = 1$ the system is integrable and the level curves of the first integral $H(x, y) := x + y - \ln y$ form a heteroclinic foliation on Q (see Section 3).

The global dynamics of the Nicholson-Bailey model (1.1) in the case when $\lambda > 1$ (which is the most interesting one from the biological viewpoint and therefore considered in mathematical biology literature) is not completely understood up to now. In particular, it is not known whether there exist periodic points in Q other than the fixed point $(\bar{p}_{\lambda}, \bar{q}_{\lambda}) := (\ln \lambda, \frac{\lambda \ln \lambda}{\lambda - 1})$. For some results concerning nonexistence of periodic points, see Corollary 4.3 for small periods, while Corollaries 4.6 and 4.7 for f_{λ} with $\lambda > 1$ close to 1. It seems that the difficulties in studying this case are related with a "huge" nonlinearity at the origin, which may be regarded as a degenerate saddle on the boundary of Q with eigenvalues 0 and λ . In the literature [5], [11], [14], [18], local spiral oscillations in a neighborhood of the fixed point $(\bar{p}_{\lambda}, \bar{q}_{\lambda})$ are described, which is based on the fact that this fixed point is an unstable focus. On the other hand, computer simulations indicate that most forward orbits exhibit divergence oscillations. In Section 4, we are able to prove rigorously the global strict oscillations for both forward and backward iterates. Moreover, Theorem 4.4 below shows that in polar coordinates centered at $(\bar{p}_{\lambda}, \bar{q}_{\lambda})$, the sequence of angles corresponding to the iterates is strictly decreasing.

By identifying $Q \setminus \{\bar{p}_{\lambda}, \bar{q}_{\lambda}\}$ with an open annulus (after appropriate scaling the radii for the polar coordinate system), Theorem 4.4 implies that if there exists an invariant circle of the form $graph(\theta)$, where θ is the angular coordinate, then on such an invariant circle the map (1.1) induces an order preserving homeomorphism, and so it has a well defined rotation number. The latter property reminds a similar property for area preserving twist maps of annulus (refer to [8]). However the Nicholson-Bailey model satisfies neither area preserving nor twist condition, and therefore the well developed KAM theory cannot be applied here. Note that there are some host-parasite models (under some biological assumptions slightly different

from those for the Nicholson-Bailey model) which produce area preserving twist maps (see [4], [12]). As for the problem of divergence in the radial coordinate or possible chaotic behavior of orbits of (1.1) for $\lambda > 1$, it still remains an open question.

In Section 5, we examine more closely for parameters region $0 < \lambda - 1 \ll 1$, the behavior of certain class of general discrete dynamical systems which includes the Nicholson-Bailey model. In this situation, the system can be viewed as a singularly perturbed one. We first establish the phenomenon of stability loss for a certain general discrete dynamical systems. This phenomenon is well known for continuous flows (see [9, 13, 17] and [2, 3]). Here we extend it to discrete maps as follows. Consider a family of systems of the form

$$x_{n+1} = F(x_n, y_n; \lambda),$$

$$y_{n+1} = G(x_n, y_n; \lambda),$$

where parameter λ runs over some interval of the real line containing $\lambda = 1$, $(F(x,y;\lambda),G(x,y;\lambda))$ is a diffeomorphism on $\{(x,y): x \geq 0, y > 0\}$ for any λ , and for each (x, y), both $F(x, y; \lambda)$ and $G(x, y; \lambda)$ are differentiable functions of λ . Assume that the set $\{(0,y): y > 0\}$ is invariant for all λ (see the hypothesis (H1) in Section 5) and, on $\{(0, y) : y > 0\}$, y_n is increasing for $\lambda > 1$ (see (H3)), and for $\lambda = 1$, the set $\{(0, y) : y > 0\}$ consists of fixed points and there exists $y^* > 0$ such that $\{(0, y) : y < y^*\}$ is stable and $\{(0, y) : y > y^*\}$ is unstable (see (H2)). Then, roughly speaking, when $0 < \lambda - 1 \ll 1$, a trajectory of the system starting at a point (x_0, y_0) with x_0 small and $y_0 < y^*$ will first be attracted toward $\{(0, y) : 0 < y < y^*\}$, second follow nearly a trajectory on $\{(0, y) : y > 0\}$ and then be repelled away from $\{(0, y) : y > y^*\}$. More precisely, there exist $\lambda_0 > 1$ and $\rho_0 > 0$ such that for $1 < \lambda < \lambda_0$, any trajectory starting at (x_0, y_0) with $0 < x_0 < \rho_0, y_0 < y^*$ will exit necessarily the strip $0 < x < \rho_0$ at some moment, say $N(\lambda)$, and at this moment $y_{N(\lambda)} > y^*$. The delay of stability loss establishes the relation between the entrance point (x_0, y_0) and the exit point $(x_{N(\lambda)}, y_{N(\lambda)})$. It states that the limit $\lim_{\lambda \to 1^+} y_{N(\lambda)}$ exists and is equal approximately (with the better accuracy for the smaller ρ_0 to the value $P(y_0)$ which is given by

$$\int_{y_0}^{P(y_0)} \frac{\ln \frac{\partial F}{\partial x}(0,y;1)}{\frac{\partial G}{\partial \lambda}(0,y;1)} \, dy = 0$$

(for more precise statement see Theorem 5.2; note that the value $P(y_0)$ is well defined due to **(H4)**).

We then apply this result to the problem of nonexistence of periodic orbits for the Nicholson-Bailey model. Comparing with the above mentioned nonexistence of periodic orbits with small period, this result (see Corollary 5.3) states that, if \tilde{R}_1 (resp. \tilde{R}_2) is the region bounded by the level curve $H(x,y) = c_1$ (resp. $H(x,y) = c_2$) and the y-axis, where $c_1 > 1$ is arbitrarily close to one (and thus \tilde{R}_1 is an arbitrarily small region) and c_2 is arbitrarily large, then there exists $\tilde{\lambda} > 1$ such that the Nicholson-Bailey model (1.1) with $1 < \lambda < \tilde{\lambda}$ has no periodic orbit of any period that is contained entirely in \tilde{R}_2 and visits $\tilde{R}_2 \setminus \tilde{R}_1$ at least once. The underlying reason is that, due to the delay of stability loss, the value of the level curve H will be increased by at least a fixed positive amount under a portion of iterations which pass close to the y-axis. In the Appendix, we show that the following interesting property takes place for maps (1.1) with $\lambda > 1$: the center of mass for all periodic and bounded orbits is the same and it coincides with the (unstable) fixed point $(\bar{p}_{\lambda}, \bar{q}_{\lambda})$.

2. **Preliminaries and simple dynamics for** $\lambda < 1$ **.** Let \mathbb{R}^2_+ be the first quadrant of the plane, i.e., $\mathbb{R}^2_+ = \{(x, y) : x \ge 0, y \ge 0\}$, and let Q be the interior of \mathbb{R}^2_+ . The Nicholson-Bailey model (1.1) is a one-parameter family of maps $f_\lambda : \mathbb{R}^2_+ \to \mathbb{R}^2_+$ with parameter $\lambda > 0$ defined by

$$f_{\lambda}(x,y) = (y(1-e^{-x}), \lambda y e^{-x}).$$
(2.2)

Then f_{λ} is one-to-one on \mathbb{R}^2_+ except the x-axis and its inverse is given by

$$f_{\lambda}^{-1}(x,y) = \left(\ln\left(1 + \frac{\lambda x}{y}\right), x + \frac{y}{\lambda}\right).$$
(2.3)

Let $J_{f_{\lambda}}(x, y)$ denote the Jacobian matrix of f_{λ} at the point (x, y), i.e.,

$$J_{f_{\lambda}}(x,y) = \begin{bmatrix} ye^{-x} & 1-e^{-x} \\ -\lambda ye^{-x} & \lambda e^{-x} \end{bmatrix}.$$

Then its determinant is equal to $\lambda y e^{-x}$. Thus f_{λ} is a diffeomorphism on $\mathbb{R}^2_+ \setminus \{(x, y) : y \neq 0\}$ (also on Q).

In what follows we denote by $(x_n(\lambda), y_n(\lambda))$ the *n*th iterate of the initial point (x_0, y_0) under the map f_{λ} . For convenience, given fixed λ , we denote $(x_n(\lambda), y_n(\lambda))$ by (x_n, y_n) . By (2.2), we have $y_{n+1} = \lambda y_n e^{-x_n}$ and so $x_n = \ln(\lambda y_n) - \ln y_{n+1}$. On the other hand, by (2.3), we have $y_{n-1} = x_n + \frac{y_n}{\lambda}$ and so $x_n = y_{n-1} - \frac{y_n}{\lambda}$. Thus we get a difference delay equation which is equivalent to (2.2):

$$\lambda y_{n-1} - y_n = \lambda \left(\ln(\lambda y_n) - \ln y_{n+1} \right). \tag{2.4}$$

It is obvious that for any λ , the origin (0,0) is a fixed point of f_{λ} , and the nonnegative y-axis is an invariant set. The dynamics of f_{λ} restricted to the nonnegative y-axis is very clear: under forward iterates of f_{λ} , every point approaches the fixed point (0,0) exponentially provided $0 < \lambda < 1$; it tends to $+\infty$ exponentially provided $\lambda > 1$; and the whole y-axis consists of fixed points provided $\lambda = 1$. So we will be concerned mainly with dynamical behavior of f_{λ} on Q.

For $0 < \lambda < 1$, the dynamics of f_{λ} on Q is very simple: the forward orbit of every point approaches the origin exponentially, while the backward orbit tends to infinity exponentially. Indeed, for forward orbit, one has $y_n = \lambda y_{n-1}e^{-x_{n-1}} < \lambda y_{n-1} < \lambda^2 y_{n-2} < \cdots < \lambda^n y_0 \to 0$ as $n \to +\infty$ and so $x_n = y_{n-1}(1 - e^{-x_{n-1}}) < y_{n-1} \to 0$ as $n \to +\infty$. For the backward orbit the same arguments show that $y_{-n} > \lambda^{-n} y_0 \to +\infty$ as $n \to +\infty$. As for x_{-n} , it can be shown that $x_{-n} \to 0$ exponentially as $n \to +\infty$. Indeed, from (2.3) we have $x_{-(n+1)} = \ln(1 + \frac{\lambda x_{-n}}{y_n}) < \frac{\lambda x_{-n}}{y_{-n}} < x_{-n}$ for sufficiently large n because $y_{-n} \to +\infty$. Hence the sequence x_{-n} is bounded, by some number, say B. Then $x_{-(n+1)} < \frac{\lambda B}{y_{-n}} < \frac{\lambda^{n+1}B}{y_0} \to 0$ as $n \to +\infty$.

3. Integrable case: heteroclinic foliation for $\lambda = 1$. As λ increases and attains the value $\lambda = 1$, the system undergoes a bifurcation as follows. At the bifurcational moment $\lambda = 1$, the set of fixed points of f_1 is the whole nonnegative y-axis. The Jacobian matrix at the point (0, y) is equal to

$$J_{f_1}(0,y) = \begin{bmatrix} y & 0\\ -y & 1 \end{bmatrix}$$

and its eigenvalues are 1 and y. Thus, every point (0, y) is a nonhyperbolic fixed point.

Let us recall the definitions of global stable and unstable manifolds. Given a fixed point p of the diffeomorphism g on the manifold M, one denotes $W_g^s(p) = \{z \in M : dist(g^n(z), p) \to 0 \text{ as } n \to +\infty\}$ and $W_g^u(p) = \{z \in M : dist(g^n(z), p) \to 0 \text{ as } n \to -\infty\}$; $W_g^s(p)$ and $W_g^u(p)$ are called the global stable and unstable manifolds of p for g, respectively (see [8] or [16]).

Usually, in the case when fixed points of a given diffeomorphism are nonhyperbolic, one succeeds very rarely in obtaining explicit expressions for the stable, unstable and center manifolds. Fortunately, in our case when $\lambda = 1$, as we will show now, the system is integrable, and the global stable and unstable manifolds of the fixed points can be described by explicit equations. To this end we need the following notation. For any y > 0 with $y \neq 1$, let $\tau(y)$ be the value different from y and defined by the equation

$$y - \ln y = \tau(y) - \ln \tau(y)$$

It is easy to see that τ is an involution of $\{y \in \mathbb{R} : y > 0, y \neq 1\}$. Now we state the result on heteroclinic foliation.

Theorem 3.1. At the bifurcational moment $\lambda = 1$, the following holds:

- 1. the function $H(x, y) := x + y \ln y$ is a first integral of the system (2.2);
- 2. if 0 < y < 1 then $W_{f_1}^u(0, y) = \{(0, y)\}$ and

$$W_{f_1}^s(0,y) \setminus \{(0,y)\} = W_{f_1}^u(0,\tau(y)) \setminus \{(0,\tau(y))\} \\ = \{(\ln t - t + y - \ln y, t) : t \in (y,\tau(y))\};\$$

3. if y > 1 then $W_{f_1}^s(0, y) = \{(0, y)\}$ and

$$W_{f_1}^u(0,y) \setminus \{(0,y)\} = W_{(0,\tau(y))}^s(f_1) \setminus \{(0,\tau(y))\}$$

= $\{(\ln t - t + y - \ln y, t) : t \in (\tau(y), y)\}$

Proof. For item 1, we show that $H(x_1, y_1) = H(x_0, y_0)$ for each $(x_0, y_0) \in Q$. Indeed, one has

$$H(x_1, y_1) = y_0(1 - e^{-x_0}) + y_0 e^{-x_0} - \ln(y_0 e^{-x_0}) = y_0 - \ln y_0 + x_0 = H(x_0, y_0)$$

and the result follows.

Next, we establish items 2 and 3. By item 1, at the bifurcational moment the whole quadrant Q splits into invariant curves of the form $x + y - \ln y = c$, where the parameter c serves as the index of the appropriate curve, $1 < c < \infty$ (because $y > 1 + \ln y$ for any $y \neq 1$). Let us fix some point $(x_0, y_0) \in Q$ and denote $c_0 = x_0 + y_0 - \ln y_0$. Then by using item 1, one gets that for any $n \in \mathbb{Z}$,

$$y_{n+1} = y_n e^{-x_n} = e^{-c_0} e^{y_n}.$$

This implies that y_n is a monotonically decreasing sequence, and moreover, that y_n is governed by the following one-dimensional map $y \mapsto e^{-c_0}e^y$ on the interval (c_-, c_+) , where c_-, c_+ are the two roots of the equation

$$y - \ln y = c_0.$$

Thus y_n tends to c_- (resp. to c_+) as $n \to +\infty$ (resp. as $n \to -\infty$). Therefore, $\lim_{n\to+\infty}(x_n, y_n) = (0, c_-)$ and $\lim_{n\to-\infty}(x_n, y_n) = (0, c_+)$. This together with item 1 implies the desired results of items 2 and 3.

Due to Theorem 3.1, we have a heteroclinic foliation on Q as the family of curves

$$\{(\ln t - t + c - \ln c, t) : t \in (c, \tau(c))\},\$$

indexed by c, where c runs over the interval (0, 1); see Figure 1. The positive y-axis serves as the center manifold for every point (0, y), $y \neq 1$.



4. Global strict oscillations on Q for $\lambda > 1$. First we consider local behavior near the positive fixed point for $\lambda > 1$. By solving the equation $f_{\lambda}(x, y) = (x, y)$, one gets that the fixed points of f_{λ} are (0,0) and $(\ln \lambda, \frac{\lambda \ln \lambda}{\lambda - 1})$. At the fixed point (0,0), the Jacobian matrix $J_{f_{\lambda}}(0,0)$ has eigenvalues 0 and λ with eigenvectors $(1,0)^T$ and $(0,1)^T$, respectively, where by v^T we denote the transport of the vector v. Thus the origin (0,0) may be regarded as a "degenerate saddle" with the x-axis as the stable manifold and the y-axis as the unstable manifold. At the other (nondegenerate) fixed point $(\ln \lambda, \frac{\lambda \ln \lambda}{\lambda - 1})$, denoted by $(\bar{p}_{\lambda}, \bar{q}_{\lambda})$, the Jacobian matrix $J_{f_{\lambda}}(\bar{p}_{\lambda}, \bar{q}_{\lambda})$ has eigenvalues

$$\mu_{\pm} = \frac{1 + \frac{\ln\lambda}{\lambda - 1} \pm \sqrt{\left(1 + \frac{\ln\lambda}{\lambda - 1}\right)^2 - 4\left(\frac{\lambda\ln\lambda}{\lambda - 1}\right)}}{2}.$$

The eigenvalues μ_{\pm} are complex numbers with modulus $\|\mu_{\pm}\| > 1$; indeed, for $\lambda > 1$, one has $\frac{\lambda \ln \lambda}{\lambda - 1} > 1$ and the function $\lambda \mapsto \frac{\ln \lambda}{\lambda - 1}$ is strictly decreasing with the maximal value 1. Therefore, the fixed point $(\bar{p}_{\lambda}, \bar{q}_{\lambda})$ is an unstable focus.

In bifurcational terms, one may say that as the parameter λ becomes bigger than 1, the points on the positive y-axis (i.e., the points which were nonhyperbolic fixed ones at the moment $\lambda = 1$) become lying on the unstable manifold of the origin, while from the singular fixed point (0,1) there appears an unstable focus $(\bar{p}_{\lambda}, \bar{q}_{\lambda}) = (\ln \lambda, \frac{\lambda \ln \lambda}{\lambda - 1})$ which moves along the curve $y = \frac{x}{1 - e^{-x}}$ as λ increases (see Figures 1 and 2, where this curve is shown by the dotted line). So by the Hartman-Grobman theorem, locally in some neighborhood of the fixed point $(\bar{p}_{\lambda}, \bar{q}_{\lambda})$ one has spiral oscillation behavior of f_{λ} . We will show that strict oscillations take place, in fact globally in both directions of time.

From now on we will consider the diffeomorphism f_{λ} as acting on the open quadrant Q. Note that the following identity holds for any orbit $(x_n, y_n), n \in \mathbb{Z}$, of f_{λ} ; this identity (which will be needed in Section 5) can be regarded as an extension

of the result of item (i) in Theorem 3.1 (here, as before, $H(x, y) = x + y - \ln y$)

$$H(x_{n+1}, y_{n+1}) - H(x_n, y_n) = \frac{\lambda - 1}{\lambda} (y_{n+1} - \bar{q}_{\lambda}).$$
(4.5)

The above identity is easily verified from the definition of f_{λ} ; it means that the value of the level curve H (which is no longer an integral for $\lambda > 1$) increases (resp. decreases) under backward iterate of a point whenever the point lies below (resp. above) the horizontal line $y = \bar{q}_{\lambda}$.

Consider four regions in Q which are formed by intersections of the vertical line $x = \ln \lambda$ and the curve $y = \frac{x}{1-e^{-x}}$. It turns out that these regions correspond to the signs of the values $(x_1 - x_0)$ and $(y_1 - y_0)$; namely, denoting these (closed) regions by A, B, C, D as shown in Figure 2, it follows easily ([19]) that $x_1 > x_0$ (resp. $x_1 < x_0$) provided $(x_0, y_0) \in int(A \cup B)$ (resp. $int(C \cup D)$); and $y_1 < y_0$ (resp. $y_1 > y_0$) provided $(x_0, y_0) \in int(B \cup C)$ (resp. $int(D \cup A)$); here int stands for the interior of a set.

In the following proposition, we show some kind of monotonicity of f_{λ} when restricted to each of these regions.

Proposition 4.1. Let $\lambda > 1$ and let $(x_0, y_0) \in Q$ be any point different from $(\bar{p}_{\lambda}, \bar{q}_{\lambda})$. Then the following statements hold:

- 1. If $(x_0, y_0) \in int(A)$, then $f_{\lambda}(x_0, y_0) \in int(A \cup B)$.
- 2. If $(x_0, y_0) \in int(B)$, then $f_{\lambda}(x_0, y_0) \in int(B \cup C)$.
- 3. If $(x_0, y_0) \in int(C)$, then $f_{\lambda}(x_0, y_0) \in int(C \cup D)$.
- 4. If $(x_0, y_0) \in int(D)$, then $f_{\lambda}(x_0, y_0) \in int(D \cup A)$.

Proof. For statement 1, we assume that (x_0, y_0) satisfies

$$x_0 < \ln \lambda$$
 and $y_0 > \frac{x_0}{1 - e^{-x_0}}$. (4.6)

We have to prove that $y_1 > \frac{x_1}{1-e^{-x_1}}$, i.e., $\lambda y_0 e^{-x_0} > \frac{y_0(1-e^{-x_0})}{1-e^{-y_0(1-e^{-x_0})}}$. To prove this inequality it is sufficient to show that

$$\lambda e^{-x_0} > 1 > \frac{1 - e^{-x_0}}{1 - e^{-y_0(1 - e^{-x_0})}}.$$
(4.7)

The first inequality of (4.7) is true because of the first inequality of (4.6). The second inequality of (4.7) is equivalent to

$$1 - e^{-x_0} < 1 - e^{-y_0(1 - e^{-x_0})} \iff e^{-x_0} > e^{-y_0(1 - e^{-x_0})} \iff x_0 < y_0(1 - e^{-x_0}).$$

And the last inequality is equivalent to the second inequality of (4.6). So we have proved that int(A) is mapped into $int(A \cup B)$. If (x_0, y_0) belongs to $\partial A \setminus \{(\bar{p}_\lambda, \bar{q}_\lambda)\}$ then one of two inequalities in (4.6) becomes equality while the other does not. Thus it is still true that $y_1 > \frac{x_1}{1-e^{-x_0}}$ and so $f_\lambda(x_0, y_0) \in int(A \cup B)$. For statement 2, we have that $x_0 \ge \ln \lambda$, $y_0 \ge \frac{x_0}{(1-e^{-x_0})}$, where at least one

For statement 2, we have that $x_0 \ge \ln \lambda$, $y_0 \ge \frac{x_0}{(1-e^{-x_0})}$, where at least one inequality is strict. Thus, $x_1 = y_0(1-e^{-x_0}) \ge x_0 \ge \ln \lambda$ and at least one inequality is strict.

We omit the proofs for statements 3 and 4 because they are similar to those for statements 1 and 2, respectively.

We interpret the previous proposition in a symbolic way as follows.

Corollary 4.2. The transition graph for the map f_{λ} with $\lambda > 1$ can be shown by the following diagram, in which an arrow of the form $X \to Y$ means that $f_{\lambda}(X) \cap Y \neq \emptyset$:



Using the fact that any periodic orbit different from $(\bar{p}_{\lambda}, \bar{q}_{\lambda})$ cannot belong to a single region A, B, C or D because of monotonicity of the signs $(x_1 - x_0)$ and $(y_1 - y_0)$ for each of these regions, we get from Proposition 4.1 the following:

Corollary 4.3. The map f_{λ} has no periodic points of periods either 2 or 3.

Note that in [19], the absence of period-2 orbits was proved by another method. For the theorem below, we need the following definition [1], a sequence $[z_{-}]^{\infty}$

For the theorem below, we need the following definition [1]: a sequence $\{z_n\}_{n=0}^{\infty}$ (resp. a bisequence $\{z_n\}_{n=-\infty}^{\infty}$) of real numbers is said to be *strictly oscillatory* around $a \in \mathbb{R}$ if there exists an increasing sequence $\{n_k\}_{k=0}^{\infty}$ (resp. an increasing bisequence $\{n_k\}_{k=-\infty}^{\infty}$) of integers such that

 $(y_{n_k} - a)(y_{n_{k+1}} - a) < 0$ for all $k \in \mathbb{N}$ (resp. for all $k \in \mathbb{Z}$).

Now we are in position to state the main result on the global strict oscillations of orbits around the unstable fixed point $(\bar{p}_{\lambda}, \bar{q}_{\lambda})$.

Theorem 4.4. Let $\lambda > 1$ and $(x_0, y_0) \in Q$ be any point different from the fixed point $(\bar{p}_{\lambda}, \bar{q}_{\lambda})$. Then the bisequences $\{x_n\}_{n=-\infty}^{\infty}$ and $\{y_n\}_{n=-\infty}^{\infty}$ are strictly oscillatory around \bar{p}_{λ} and \bar{q}_{λ} respectively. Moreover, in polar coordinates (r, θ) centered at $(\bar{p}_{\lambda}, \bar{q}_{\lambda})$, for the bisequence $\{(x_n, y_n)\}_{n=-\infty}^{\infty}$ the corresponding bisequence $\{\theta_n\}_{n=-\infty}^{\infty}$ of polar angles is strictly decreasing and satisfies $\lim_{n\to\infty} \theta_n = -\infty$ and $\lim_{n\to-\infty} \theta_n = +\infty$.

Proof. Note that for any initial point (x_0, y_0) different from $(\bar{p}_{\lambda}, \bar{q}_{\lambda})$, the forward orbit can not stay eventually in a single region A, B, C or D (see Figure 2). Indeed, otherwise we would get from monotonicity of both functions $(x_1 - x_0)$ and $(y_1 - y_0)$ for each of these regions that the sequence (x_n, y_n) must approach either the fixed point $(\bar{p}_{\lambda}, \bar{q}_{\lambda})$ or infinity. But the former case is impossible because $(\bar{p}_{\lambda}, \bar{q}_{\lambda})$ is an unstable focus while in the latter case (x_n, y_n) must stay in the region A with $\lim_{n\to\infty} x_n = \hat{x}$, $\lim_{n\to\infty} y_n = +\infty$ for some $0 < \hat{x} \leq \bar{p}_{\lambda}$, which is also impossible due to (2.2). Now Corollary 4.2 implies immediately that the sequences $\{x_n\}_{n=0}^{\infty}$ and $\{y_n\}_{n=0}^{\infty}$ are strict oscillatory and also that $\lim_{n\to\infty} \theta_n = -\infty$. It remains to consider backward iterates and to prove the strict monotonicity of θ_n .

It will be more convenient to study iterates of f_{λ}^{-1} instead of those of f_{λ} . Let $(u, v) = T(x, y) = (x + \frac{y}{\lambda} - \bar{q}_{\lambda}, y - \bar{q}_{\lambda})$ be the linear affine transformation for Q, then in the new coordinates, $\tilde{f}_{\lambda}^{-1}(u, v) := T \circ f_{\lambda}^{-1} \circ T^{-1}(u, v)$ takes the form

$$\tilde{f}_{\lambda}^{-1}(u,v) = \left(\frac{u}{\lambda} + \ln\left(\frac{u + \bar{q}_{\lambda}}{v + \bar{q}_{\lambda}}\right), u\right)$$

and maps T(Q) onto T(Q). It is easy to check that $T(\bar{p}_{\lambda}, \bar{q}_{\lambda}) = (0, 0)$ and

$$T(Q) = \{(u, v) : u > -\bar{q}_{\lambda}, \quad -\bar{q}_{\lambda} < v < \lambda u + (\lambda - 1)\bar{q}_{\lambda}\}.$$

Consider the straight line v = ku with slope $k \ge 0$ on the (u, v)-plane and denote $(\hat{u}, \hat{v}) = \tilde{f}_{\lambda}^{-1}(u, v)$. Then \tilde{f}_{λ}^{-1} maps the intersection of this straight line with T(Q) onto the intersection of the following curve $\hat{u}(\hat{v})$

$$\hat{u} = \frac{\hat{v}}{\lambda} + \ln\left(\frac{\hat{v} + \bar{q}_{\lambda}}{k\hat{v} + \bar{q}_{\lambda}}\right) \tag{4.8}$$

with T(Q) (on the (\hat{u}, \hat{v}) -plane). First we show

Claim 1: the curve (4.8) considered as the graph of a function of \hat{v} on the (\hat{v}, \hat{u}) plane (i.e., with \hat{v} -axis as the horizontal one) is concave upward if k > 1, concave downward if $0 \le k < 1$, and straight if k = 1. Indeed, by simple calculations, we have that

$$\frac{\partial^2 \hat{u}}{\partial \hat{v}^2}(\hat{v}) = \frac{\bar{q}_\lambda(k-1)[2k\hat{v} + \bar{q}_\lambda(k+1)]}{(\hat{v} + \bar{q}_\lambda)^2(k\hat{v} + \bar{q}_\lambda)^2}.$$
(4.9)

If k > 1, then from the equations for the boundary of T(Q), it follows that $v = ku > -\bar{q}_{\lambda}$ and thus $\hat{v} = u > -\frac{\bar{q}_{\lambda}}{k}$. Therefore we have $2k\hat{v} + \bar{q}_{\lambda}(k+1) > \bar{q}_{\lambda}(k-1) > 0$ and $\frac{\partial^2 \hat{u}}{\partial \hat{v}^2}(\hat{v}) > 0$. If $0 \le k < 1$, then again from the equations for the boundary of T(Q), it follows that $v = ku < \lambda u + (\lambda - 1)\bar{q}_{\lambda}$ and thus $\hat{v} = u > \frac{\lambda - 1}{k - \lambda}\bar{q}_{\lambda}$. Therefore we have $2k\hat{v} + \bar{q}_{\lambda}(k+1) \ge \frac{\bar{q}_{\lambda}(1-k)(\lambda+k)}{\lambda-k} > 0$ and $\frac{\partial^2 \hat{u}}{\partial \hat{v}^2}(\hat{v}) < 0$. For two exceptional cases of the straight lines v = u and u = 0, their \tilde{f}_{λ}^{-1} -images are again straight lines, $\hat{v} = \lambda \hat{u}$ and $\hat{v} = 0$ respectively.

From now on we will consider the curve (4.8) as lying again in T(Q) on the (u, v)-plane, i.e., we rewrite (4.8) as

$$u = \frac{v}{\lambda} + \ln\left(\frac{v + \bar{q}_{\lambda}}{kv + \bar{q}_{\lambda}}\right) \tag{4.10}$$

Next we show

Claim 2: the line v = ku intersects its \tilde{f}_{λ}^{-1} -image, the curve (4.10), only at the origin in T(Q).

To this end, first consider the case when $1 < k \leq \lambda$ and take the difference between *u*-coordinates for these two curves as the function of v. We then claim that such a function $h_k(v) := \frac{1}{k}v - \left(\frac{v}{\lambda} + \ln(\frac{v+\bar{q}_{\lambda}}{kv+\bar{q}_{\lambda}})\right)$ is strictly increasing for all $v \geq -\bar{q}_{\lambda}$. Indeed, we have

$$\frac{\partial h_k}{\partial v}(v) = \frac{\lambda - k}{k\lambda} - \frac{\bar{q}_\lambda(1 - k)}{(v + \bar{q}_\lambda)(kv + \bar{q}_\lambda)} > 0.$$
(4.11)

Next, we consider the case when $0 < k \leq 1$ and define $h_k(v)$ for $v \geq 0$ as above. Then the value $\frac{\partial h_k}{\partial v}(v)$ in (4.11) with $v \geq 0$ is also positive because $\frac{\partial^2 h_k}{\partial v^2}(v) = -\frac{\partial^2 u}{\partial v^2}(v)$, where u(v) is the function (4.10), and so by Claim 1, $\frac{\partial^2 h_k}{\partial v^2}(v) \geq 0$; and besides $\frac{\partial h_k}{\partial v}(0) > 0$ (for the latter inequality we note that $\frac{\partial}{\partial k}\left(\frac{\partial h_k}{\partial v}(0)\right) = -\frac{1}{k^2} + \frac{1}{\bar{q}_\lambda} < 0$ and $\frac{\partial h_1}{\partial v}(0) = 1 - \frac{1}{\lambda} > 0$). For v < 0 we have the finite part, say α , of the curve (4.10) in T(Q) with two end points: namely, the origin and a point on the boundary straight line $v = \lambda u + (\lambda - 1)\bar{q}_\lambda$. Note that the latter point lies strictly below the initial straight line v = ku (with respect to the (u, v)-plane, and so it lies strictly above with respect to the (v, u)-plane). Hence by Claim 1, the whole α lies below v = ku and so Claim 2 follows for this case. Now for $k > \lambda$, we have that the intersection of the line v = ku with T(Q) is the line segment v = ku with $-\bar{q}_{\lambda} < v < \frac{k(\lambda-1)\bar{q}_{\lambda}}{k-\lambda}$, and we need to check that this line segment intersects its \tilde{f}_{λ}^{-1} -image at the origin only. But this is a consequence of upward concavity (with respect to the (v, u)-plane) of this image along with a simple calculation for the images of end points of this segment. At last, for $k \leq 0$ the result is trivial because \tilde{f}_{λ}^{-1} maps the points from the second and fourth quadrants on (u, v)-plane into points in the third and first quadrants respectively. We have completed the proof of Claim 2.

Using the fact that by the Hartman-Grobman theorem, in a small neighborhood of the origin, \tilde{f}_{λ}^{-1} is topologically conjugate to a hyperbolic linear map on \mathbb{R}^2 having the stable focus type, the above arguments prove strict monotonicity in polar angle for iterates of \tilde{f}_{λ}^{-1} (and thus for iterates of f_{λ} as well). Finally we show that for any forward \tilde{f}_{λ}^{-1} -orbit, say γ^+ , of a point different

Finally we show that for any forward f_{λ}^{-1} -orbit, say γ^+ , of a point different from the origin, the corresponding sequence of polar angles is unbounded. Suppose the contrary. Then using the obtained fact that the sequence of polar angles is monotone increasing, we have that this orbit γ^+ should stay eventually in an arbitrarily small cone which is bounded by two close polar rays on the (u, v)-plane, say $\theta = \varphi_0$ and $\theta = \varphi_0 - \varepsilon_0$ with ε_0 small. Let us denote such a cone by $K_{\varphi_0,\varepsilon_0}$. Since the *v*-axis is mapped by \tilde{f}_{λ}^{-1} to the *u*-axis, the second and fourth quadrants in (u, v)-plane cannot contain $K_{\varphi_0,\varepsilon_0}$, i.e., $\tan \varphi_0$ cannot be negative. Note that the angle between each ray through the origin and the tangent direction at the origin of the \tilde{f}_{λ}^{-1} -image of this ray is uniformly bounded away from zero; indeed, this can be observed by the Hartman-Grobman theorem or by simple calculation (see also formula (4.12) below). By this and the concavity of the \tilde{f}_{λ}^{-1} -image of straight lines through the origin (see the proof of Claim 1) we get the following: if $0 < \varphi_0 \leq \frac{\pi}{4}$ or $\arctan(\lambda) < \varphi_0 < \frac{\pi}{2}$ or $\pi < \varphi_0 < \frac{3}{2}\pi$ (with ε_0 sufficiently small), then $\tilde{f}_{\lambda}^{-1}(K_{\varphi_0,\varepsilon_0})$ is contained in a come which has no intersection with $K_{\varphi_0,\varepsilon_0}$ except at the origin. So in these cases $\tilde{f}_{\lambda}^{-1}(K_{\varphi_0,\varepsilon_0}) \cap K_{\varphi_0,\varepsilon_0} = \{(0,0)\}$, which contradicts the definition of $K_{\varphi_0,\varepsilon_0}$. Thus it remains to consider the last case when $\frac{\pi}{4} < \varphi_0 \leq \arctan(\lambda)$. In this case we have that $\tilde{f}_{\lambda}^{-1}(K_{\varphi_0,\varepsilon_0})$ is a region in T(Q) bounded by two concave curves

$$u = \frac{v}{\lambda} + \ln\left(\frac{v + \bar{q}_{\lambda}}{v \tan(\varphi_0 - \varepsilon_0) + \bar{q}_{\lambda}}\right) \text{ and } u = \frac{v}{\lambda} + \ln\left(\frac{v + \bar{q}_{\lambda}}{v \tan(\varphi_0) + \bar{q}_{\lambda}}\right),$$

where $v \ge 0$. These two curves are asymptotic (as $v \to +\infty$) to the straight lines $v = \lambda u + \lambda \ln (\tan(\varphi_0 - \varepsilon_0))$ and $v = \lambda u + \lambda \ln (\tan(\varphi_0))$, which lie outside $K_{\varphi_0,\varepsilon_0}$. So we get again $\tilde{f}_{\lambda}^{-1}(K_{\varphi_0,\varepsilon_0}) \bigcap K_{\varphi_0,\varepsilon_0} = \{(0,0)\}$. The obtained contradiction completes the proof of the theorem.

Given a real number $\varphi_0 \in [0, 2\pi)$, let R_{φ_0} be the ray in Q which is defined by the equation $\theta = \varphi_0$ in polar coordinates (r, θ) centered at $(\bar{p}_\lambda, \bar{q}_\lambda)$. By Theorem 4.4, $f_\lambda^{-1}(R_{\varphi_0}) \cap R_{\varphi_0} = \{(\bar{p}_\lambda, \bar{q}_\lambda)\}$, and the curves R_{φ_0} and $f_\lambda^{-1}(R_{\varphi_0})$ bound a (simply connected) region, denoted by D_{φ_0} , in Q; more precisely, D_{φ_0} is that of two regions bounded by R_{φ_0} and $f_\lambda^{-1}(R_{\varphi_0})$ which has nonempty intersection with the rays $\theta = \varphi_0 + \epsilon$ for any sufficiently small ϵ . The following is an immediate consequence of Theorem 4.4.

Corollary 4.5. For any $\varphi_0 \in [0, 2\pi)$ and any initial point $(x_0, y_0) \in Q$, both forward and backward orbits of (x_0, y_0) under f_{λ} with $\lambda > 1$ visit D_{φ_0} infinitely many times.

Another consequence of Theorem 4.4 is the following result on nonexistence of periodic points for f_{λ} with λ close to one.

Corollary 4.6. For any positive integer N, there exists $\lambda_0 > 1$ such that for any $1 < \lambda < \lambda_0$, f_{λ} has no periodic points of period less than N except the fixed point $(\bar{p}_{\lambda}, \bar{q}_{\lambda}) = (\ln \lambda, \frac{\lambda \ln \lambda}{\lambda - 1}).$

Proof. We use notations from the proof of Theorem 4.4. Consider the ray $\{(u, v) \in T(Q) : v = ku, u \ge 0\}$ with slope k > 0. If $1 \le k < \lambda$, then the tangent line of its f_{λ}^{-1} -image at the origin is given by

$$v = \frac{u}{(1/\lambda) + (1/\bar{q}_{\lambda}) - (k/\bar{q}_{\lambda})}.$$

Now plug $\bar{q}_{\lambda} = \frac{\lambda \ln \lambda}{\lambda - 1}$ into the above equation and consider the "tangent" map

$$\psi_{\lambda}(k) := \frac{\lambda \ln \lambda}{\ln \lambda + (1-k)(\lambda-1)}.$$
(4.12)

Note that $\lim_{\lambda \searrow 1} \psi_{\lambda}(k) = \frac{1}{2-k}$ and $\lim_{k \searrow 1} \psi_{\lambda}(k) = \lambda$. Hence the function $\psi_{\lambda}(k)$ of two variables can be extended continuously to some domain $[1+\epsilon] \times [1+\epsilon]$ with $\epsilon > 0$. One can easily check that there are some positive numbers $\overline{\delta}$ and $\overline{\epsilon}$ such that for $k \in [1, 1+\overline{\delta}]$ and $\lambda \in [1, 1+\overline{\epsilon}]$, the function $\psi_{\lambda}(k)$ satisfies the following properties: (i) $\psi_{\lambda}(k)$ is C^1 (both in k and λ); (ii) $\psi_{\lambda}(k)$ is monotone increasing both in k and λ ; and (iii) $\psi_{\lambda}(k) \ge k$, where the inequality is strict if $\lambda > 1$. We also note that $\psi_{\lambda}(1) = \lambda$. Hence there is $0 < \epsilon_0 < \overline{\epsilon}$ sufficiently small such that $1 < \psi_{\lambda}^n(1) < 1 + \overline{\delta}$ for any $\lambda \in [1, 1 + \epsilon_0]$ and $n = 1, 2, \dots, N$.

Suppose (u_i, v_i) , $i \in \mathbb{Z}$, is a periodic orbit of f_{λ} with $1 < \lambda < \lambda_0 := 1 + \epsilon_0$. By Corollary 4.5, we may assume that (u_0, v_0) belongs to the cone $\{(u, v) \in T(Q) : u > 0, u \leq v \leq \lambda u\}$. Since for straight lines with slopes bigger than 1, their \tilde{f}_{λ}^{-1} -images are concave upward curves (see Claim 1 in the proof of Theorem 4.4), the above arguments show that for each $n = 1, 2, \ldots, N$ the point (u_n, v_n) belongs to the cone bounded by the rays $v = \lambda u$ and $v = \psi_{\lambda}^n(1)u$, u > 0, and so all the points (u_n, v_n) with $n = 1, 2, \ldots, N$ belong to the cone bounded by the rays $v = \lambda u$ and $v = (1 + \bar{\delta})u$, u > 0. So the period of (u_0, v_0) must be bigger than N.

Together with Corollary 4.2, Theorem 4.4 also implies that f_{λ} , with λ close to one, has no periodic orbit away from small neighborhood of the point (0, 1).

Corollary 4.7. Let U_{ρ} denote the disk of radius ρ centered at (0,1) in the xy-plane. Then for any $\rho > 0$ there exists $\tilde{\lambda} > 0$ such that for every $1 < \lambda < \tilde{\lambda}$, both forward and backward orbits of f_{λ} visit U_{ρ} infinitely many times; in particular, f_{λ} has no periodic orbit entirely in $Q \setminus U_{\rho}$.

Proof. Let S_{ρ} be the semicircle which is the boundary of $Q \cap U_{\rho}$ in Q. Consider the intersection point of S_{ρ} with the curve $y = x/(1 - e^{-x})$, i.e., with the curve of fixed points $(\ln \lambda, \frac{\lambda \ln \lambda}{\lambda - 1})$ of f_{λ} for $\lambda > 1$ as the parameter of the curve (see Figure 2), and let λ_{ρ} be the corresponding value of λ for this intersection point. For $1 < \lambda \leq \lambda_{\rho}$, let us denote by $y_{\lambda}^{-} < 1$ and $y_{\lambda}^{+} > 1$ the y-coordinates for the two intersection

points of S_{ρ} with the vertical line $x = \ln \lambda$. It is easy to see that $y_{\lambda}^{-} < y_{\lambda_{\rho}}^{-}$ and $y_{\lambda}^{+} < y_{\lambda_{\rho}}^{+}$ for $1 < \lambda < \lambda_{\rho}$. Furthermore, we define $\tilde{\lambda} := \min\left\{\lambda_{\rho}, \frac{y_{\lambda_{\rho}}^{+}}{y_{\lambda_{\rho}}^{-}}\right\}$.

Now suppose by the contrary that there is a forward orbit $\{(x_n, y_n)\}_{n=0}^{\infty}$ of f_{λ} with $1 < \lambda < \tilde{\lambda}$ which visits U_{ρ} only finitely many times, i.e., $(x_n, y_n) \notin U_{\rho}$ for all n > m, where m is some constant. Then it follows from Corollary 4.2 and Theorem 4.4, that for some positive iterate $n_0 \ge m$ one has that $(x_{n_0}, y_{n_0}) \in D \setminus U_{\rho}$ and $(x_{n_0+1}, y_{n_0+1}) \in A \setminus U_{\rho}$ (see Figure 2). But this contradicts to the following:

$$y_{n_0+1} = \lambda y_{n_0} e^{-x_{n_0}} < \frac{y_{\lambda_\rho}^+}{y_{\lambda_\rho}^-} \cdot y_{\lambda}^- \cdot 1 < y_{\lambda_\rho}^+,$$

while $y_{n_0+1} \ge y_{\lambda}^+ > y_{\lambda_{\rho}}^+$. The result for the backward orbits is obtained in similar way.

For more information about nonexistence of periodic orbit for λ close to one, see Corollary 5.3 in the next section.

5. Delay of stability loss for general discrete dynamical systems and application to the Nicholson-Bailey model. In this section, we describe the delay of stability loss for discrete dynamical systems and then give an application to the Nicholson-Bailey model.

Consider the family of discrete dynamical systems

$$\begin{aligned}
x_{n+1} &= F(x_n, y_n; \lambda), \\
y_{n+1} &= G(x_n, y_n; \lambda),
\end{aligned}$$
(5.13)

where parameter λ runs over some interval of the real line containing $\lambda = 1$, $(F(x, y; \lambda), G(x, y; \lambda))$ is a diffeomorphism on $\{(x, y) : x \geq 0, y > 0\}$ for each λ , and $F(x, y; \lambda)$ and $G(x, y; \lambda)$ are both C^2 functions in (x, y, λ) and satisfy the following hypotheses:

- (H1) $F(0, y; \lambda) = 0$ for all y and λ ;
- (H2) there exists $y^* > 0$ such that $F_x(0, y; 1) > 0$ for all y and

$$F_x(0,y;1) = \begin{cases} < 1, & \text{for } y < y^*, \\ = 1, & \text{for } y = y^*, \\ > 1, & \text{for } y > y^*; \end{cases}$$

- **(H3)** G(0, y; 1) = y and $G_{\lambda}(0, y; 1) > 0$ for all y and λ ;
- (H4) for the above y^* , if $0 < y < y^*$ there exists a finite number, denoted by P(y), such that $P(y) \neq y$ and

$$\int_{y}^{P(y)} \frac{\ln F_x(0,t;1)}{G_\lambda(0,t;1)} dt = 0.$$
(5.14)

Note that $y \mapsto P(y)$ is a well-defined function from the interval $(0, y^*)$ to the interval $(y^*, +\infty)$ and is independent of λ . Here we use the notations F_x and G_λ for the derivatives with respect to variables (while f_λ still denotes a one-parameter family of maps as in (2.2)).

In view of the hypotheses (H1)-(H3), for λ close to one, the variable y varies slowly and the variable x varies fast. Thus, for λ close to one, we will view the dynamical system (5.13) as a singularly perturbed problem.

We start with a discussion on the geometric property of system (5.13). For $\lambda = 1$, the set $S = \{(0, y) : y > 0\}$ consists of fixed points. It will be called the

slow manifold as in the case of singularly perturbed continuous dynamical systems. Hypothesis **(H2)** implies that any compact subset of

$$\mathcal{S}_{-} := \{ (0, y) : 0 < y < y^* \}$$

is normally stable, and any compact subset of

$$\mathcal{S}_+ := \{(0, y) : y > y^*\}$$

is normally unstable. The normal stability of the slow manifold \mathcal{S} changes across the point $(0, y^*)$. This point $(0, y^*)$ is often referred to as a turning point. The presence of this turning point on \mathcal{S} implies that \mathcal{S} is not normally hyperbolic (see [6, 7, 10). The invariant manifold theory states that a nonnormally hyperbolic invariant manifold does not persist under *general* perturbations. It is important to observe that, under the hypothesis (H1), the slow manifold \mathcal{S} stays as an invariant manifold for all λ although it is not normally hyperbolic. In addition, from the hypothesis (H3), for $\lambda > 1$, the flow on S crosses the turning point $(0, y^*)$ from the stable region \mathcal{S}_{-} to the unstable region \mathcal{S}_{+} . The turning point $(0, y^*)$ together with this property induces the phenomenon of *delay of stability loss* (see Theorem 5.2 below), which plays crucial role in the study of oscillations. It should be remarked that the invariance of S for $\lambda \neq 1$ is a special property of the perturbed system. Thus, mathematically, such a perturbation is not a generic one. On the other hand, biologically, it makes perfect sense: if the initial density of the parasites is zero, i.e., $x_0 = 0$ for the Nicholson-Bailey model, then it stays that way forever, i.e., $x_n = 0$ for all $n \in \mathbb{N}$.

Throughout this section, let $(x_n(\lambda), y_n(\lambda))$ denote the *n*th iterate of the initial point (x_0, y_0) under the system (5.13). For convenience, given fixed λ , we denote $(x_n(\lambda), y_n(\lambda))$ by (x_n, y_n) . We also denote the local stable (resp. unstable) manifold of (0, y) for $y < y^*$ (resp. $y > y^*$) under system (5.13) with $\lambda = 1$ by $W^s(0, y)$ (resp. $W^u(0, y)$). We define $y = S(x_0, y_0)$ if $(x_0, y_0) \in W^s(0, y)$; similarly, we define $y = U(x_0, y_0)$ if $(x_0, y_0) \in W^u(0, y)$.

The following lemma will be needed later.

Lemma 5.1. First, for any fixed Y_1 , Y_2 and Y_4 with $Y_1 < Y_2 < y^* < Y_4$, there exist $\rho_0 > 0$, $\delta_0 > 0$ and $\beta_2 > \beta_1 > 0$ such that $\beta_1 y \leq G_{\lambda}(x, y; \lambda) \leq \beta_2 y$ provided $0 \leq x \leq \rho_0$, $Y_1 \leq y \leq Y_4$ and $1 \leq \lambda \leq 1 + \delta_0$, and there exist Y_3 , \bar{y} and L < 1 such that $Y_2 < \bar{y} < y^* < Y_3 < Y_4$, $\bar{y}^{\beta_1 + 2\beta_2} > Y_2^{\beta_1} Y_3^{2\beta_2}$,

$$\max\{F_x(0, y; 1) : Y_1 \le y \le \bar{y}\} < L,$$

and

$$\max\{F_x(0, y; 1) : Y_2 \le y \le Y_3\} < L^{-1}.$$

Second, if $\rho > 0$ and $\delta > 0$ are small enough, then there exists a constant C > 0such that if (x_0, y_0) is an initial point for system (5.13) with $x_0 < \rho$, $y_0 < y^*$ and $Y_1 < S(x_0, y_0) < Y_2$, then for any λ with $1 < \lambda < 1 + \delta$,

- (i) there exists a unique integer $M(\lambda) > 0$ such that $y_n < y^* \le y_{M(\lambda)}$ and $x_n < \rho$ for $0 \le n < M(\lambda)$;
- (ii) there exists an integer $J(\lambda) \ge M(\lambda)$ such that $Y_3 < y_{J(\lambda)} < Y_4$ and $x_n < \rho$ for $0 \le n < J(\lambda)$;
- (iii) for the above $M(\lambda)$ and $J(\lambda)$, we have that $x_n \leq \rho e^{-Cn}$ for $0 \leq n \leq M(\lambda)$ and $x_n \leq \rho e^{-C(J(\lambda)-n)}$ for $M(\lambda) \leq n \leq J(\lambda)$.

Proof. We make several preparations for the proof. By a C^2 change of variables (see Robinson [16], p.200), we may assume that for system (5.13) with $\lambda = 1$, the local stable manifold of (0, y) for $Y_1 \leq y \leq (Y_2 + y^*)/2$ is horizontally flat, i.e.,

$$W^{s}(0, y) = \{(u, v) : v = y, 0 \le u \le \rho_1\}$$

for some $\rho_1 > 0$. So we may assume that if $0 \le x \le \rho_1$ and $Y_1 \le y \le (Y_2 + y^*)/2$, then G(x, y; 1) = G(0, y; 1) = y, and hence, by the mean value theorem,

$$G(x, y; \lambda) = G(x, y; 1) + G_{\lambda}(x, y; \overline{\lambda})(\lambda - 1)$$

= y + (G_{\lambda}(0, y; 1) + O(x) + O(\lambda - 1))(\lambda - 1). (5.15)

Moreover, since $G_{\lambda}(0, y; 1) > 0$, there exists $0 < \rho_2 < \rho_1$, $\delta_1 > 0$ and A > 0such that if $0 \le x \le \rho_2$, $Y_1 \le y \le (Y_2 + y^*)/2$ and $0 \le \lambda - 1 \le \delta_1$, then $G_{\lambda}(0, y; 1) + O(x) + O(\lambda - 1) \ge A$, and hence

$$G(x, y; \lambda) \ge y + A(\lambda - 1). \tag{5.16}$$

We first show the existence of ρ_0 , δ_0 , β_1 , β_2 , Y_3 , \bar{y} and L with the desired properties. Since $G_{\lambda}(0,y;1) > 0$, there exist $\rho_0 > 0$, $\delta_0 > 0$ and $\beta_2 > \beta_1 > 0$ such that if $0 \le x \le \rho_0$, $Y_1 \le y \le Y_4$ and $1 \le \lambda \le 1 + \delta_0$, then $\beta_1 y \le G_{\lambda}(x,y;\lambda) \le \beta_2 y$. Note that $(y^*)^{\beta_1+2\beta_2} > Y_2^{\beta_1}(y^*)^{2\beta_2}$. Thus there exist \bar{y} and y^* such that $\bar{y} < y^* < Y_3$ and $\bar{y}^{\beta_1+2\beta_2} > Y_2^{\beta_1}Y_3^{2\beta_2}$. Since $\max\{F_x(0,y;1): Y_1 \le y \le \bar{y}\} < 1$, there exists 0 < L < 1 such that $\max\{F_x(0,y;1): Y_1 \le y \le \bar{y}\} < L$. Since $F_x(0,y;1) \le 1$ for $Y_2 \le y \le y^*$, we may take a smaller Y_3 if necessary so that

$$\max\{F_x(0,y;1): Y_2 \le y \le Y_3\} < L^{-1}.$$

By the hypothesis (H3) and the mean value theorem, we have that

$$G(x, y; \lambda) = G(0, y; 1) + G_x(\bar{x}, y; \bar{\lambda})x + G_\lambda(\bar{x}, y; \bar{\lambda})(\lambda - 1)$$

= $y + G_x(\bar{x}, y; \bar{\lambda})x + G_\lambda(\bar{x}, y; \bar{\lambda})(\lambda - 1).$ (5.17)

By the continuity of G_x , there exist $\alpha_1 > 0$ and $\alpha_2 > 0$ such that if $0 \le x \le \rho_0$, $Y_1 \le y \le Y_4$ and $1 \le \lambda \le 1 + \delta_0$, then $-\alpha_1 y \le G_x(\bar{x}, y; \bar{\lambda}) \le \alpha_2 y$, and hence

$$y(1 - \alpha_1 x + \beta_1(\lambda - 1)) \le G(x, y; \lambda) \le y(1 + \alpha_2 x + \beta_2(\lambda - 1)).$$
(5.18)

For later convenience, we set $\gamma = \beta_1/(2\alpha_1)$. Due to the hypotheses **(H1)** and **(H2)**, there exist a > 0 and b > 0 such that if $Y_1 \le y \le y^*$, $0 \le x \le \rho_0$ and $1 \le \lambda \le 1 + \delta_0$, then

$$F(x, y; \lambda) = F(0, y; \lambda) + F_x(\bar{x}, y; \lambda)x = F_x(\bar{x}, y; \lambda)x$$

= $\left(F_x(0, y; 1) + F_{xx}(\tilde{x}, y; \tilde{\lambda})\bar{x} + F_{x\lambda}(\tilde{x}, y; \tilde{\lambda})(\lambda - 1)\right)x$ (5.19)
 $\leq (1 + ax + b(\lambda - 1))x.$

Since

$$\max\{F_x(0, y; 1) : Y_1 \le y \le \bar{y}\} < L < 1, \\ \max\{F_x(0, y; 1) : Y_2 \le y \le Y_3\} < L^{-1},$$

we can choose $\rho > 0$ and $\delta > 0$ with $\rho \le \min\{\rho_0, \rho_2\}$ and $\delta \le \min\{\delta_0, \delta_1\}$ such that $\gamma \delta < \rho, \ 1 + (\gamma a + b)\delta < L^{-1},$

and if $0 \leq x < \rho$ and $1 \leq \lambda \leq 1 + \delta$ then

$$|F_x(x,y;\lambda)| \le L \quad \text{for} \quad Y_1 \le y \le \bar{y};$$

$$|F_x(x,y;\lambda)| \le L^{-1} \quad \text{for} \quad Y_2 \le y \le Y_3.$$
 (5.20)

Since $\bar{y}^{\beta_1+2\beta_2} > Y_2^{\beta_1}Y_3^{2\beta_2}$, we have that

$$\frac{1}{\beta_2} \ln \frac{\bar{y}}{Y_2} > \frac{2}{\beta_1} \ln \frac{Y_3}{\bar{y}}.$$
(5.21)

Thus for $\rho > 0$ small and $\lambda > 1$ close to one,

$$\frac{(1-L)\ln(\bar{y}/Y_2) - \alpha_2\rho}{\beta_2(1-L)} > \frac{(\lambda-1)\ln(\gamma(\lambda-1))}{\ln L} + \frac{(\lambda-1)\ln(Y_3/\bar{y})}{\ln(1+\beta_1(\lambda-1)/2)} + (\lambda-1)$$
(5.22)

because that letting $\rho \to 0$ and $\lambda \to 1$, inequality (5.22) reduces to inequality (5.21). Therefore, for $0 < \rho < 1$ and $\delta > 0$ small, one has that $\frac{(\rho-1)\ln\rho}{\ln L} > 0$, and hence, if $1 < \lambda < 1 + \delta$, then

$$\frac{(1-L)\ln(\bar{y}/Y_2) - \alpha_2\rho}{\beta_2(1-L)} > \frac{(\lambda-1)\ln(\gamma(\lambda-1)/\rho)}{\ln L} + \frac{(\lambda-1)\ln(Y_3/\bar{y})}{\ln(1+\beta_1(\lambda-1)/2)} + (\lambda-1).$$
(5.23)

Now we start to prove the desired results (i)-(iii).

(i) Let $\rho > 0$ and $\delta > 0$ small as above and let (x_0, y_0) be an initial point for system (5.13) with $x_0 < \rho$, $y_0 < y^*$ and $Y_1 < S(x_0, y_0) < Y_2$. By the flatness of $W^s(0, y)$, we have $Y_1 < y_0 = S(x_0, y_0) < Y_2$. Consider the parameter λ with $1 < \lambda < 1 + \delta$. We now show the existence of $M(\lambda)$. Let n_0 be the first integer so that $0 < x_n < \rho$ for $0 \le n < n_0$ and $x_{n_0} \ge \rho$ (it will be shown that n_0 is finite). If $y_n \ge y^*$ for some $n < n_0$, then we are done. Suppose, on the contrary, that $y_n < y^*$ for $0 \le n < n_0$. We consider two cases: Case 1. $y_n \le \bar{y}$ for $0 \le n < n_0$ and Case 2. $\bar{y} \le y_n < y^*$ for some $n < n_0$.

For Case 1, first we show that $Y_1 \leq y_n \leq \overline{y}$ for all $0 \leq n < n_0$. Indeed, for $y_n \leq (Y_2 + y^*)/2$, inequality (5.16) implies that

$$y_{n+1} = y_n + A(\lambda - 1) > y_n,$$

and for $(Y_2 + y^*)/2 \le y_n \le \overline{y}$, equality (5.17) gives us that

$$y_{n+1} = y_n + G_x(\bar{x}_n, y_n; \lambda)x_n + G_\lambda(\bar{x}_n, y_n; \lambda)(\lambda - 1)$$

$$\geq (Y_2 + y^*)/2 + O(x_n) + O(\lambda - 1)$$

$$\geq Y_1;$$

for the last inequality we take smaller ρ and δ if necessary. Next by (5.20), we have that for $0 \le n < n_0$,

$$x_{n+1} = F(x_n, y_n; \lambda) = F(0, y_n; \lambda) + F_x(\bar{x}_n, y_n; \lambda) x_n$$
$$\leq L x_n \leq \dots \leq L^{n+1} x_0 = x_0 e^{(n+1) \ln L};$$

in particular, $x_{n_0} \leq x_0 e^{n_0 \ln L} < \rho$. This contradicts to the choice of n_0 .

For Case 2, let $n_1 < n_0$ be the first integer so that $y_{n_1} \ge \bar{y}$ and $y_n < \bar{y}$ for $0 \le n < n_1$. As estimated in Case 1, for $0 \le n < n_0$, we have $Y_1 \le y_n \le y^*$; moreover, for $0 \le n < n_1$, we get $Y_1 \le y_n \le \bar{y}$ and $x_{n+1} \le x_0 L^{n+1} < \rho L^{n+1}$. Thus

by (5.18), we get that for $0 \le n < n_1$,

$$y_{n+1} = G(x_n, y_n; \lambda) \le y_n (1 + \alpha_2 x_n + \beta_2 (\lambda - 1))$$

$$\le y_0 \prod_{k=0}^n (1 + \alpha_2 x_k + \beta_2 (\lambda - 1))$$

$$\le y_0 \exp\left\{\sum_{k=0}^n \ln(1 + \alpha_2 x_k + \beta_2 (\lambda - 1))\right\}$$

$$\le y_0 \exp\left\{\sum_{k=0}^n \alpha_2 x_k + \sum_{k=0}^n \beta_2 (\lambda - 1)\right\}$$

$$\le y_0 \exp\left\{\alpha_2 \rho \sum_{k=0}^n L^k + \sum_{k=0}^n \beta_2 (\lambda - 1)\right\}$$

$$\le y_0 \exp\left\{\frac{\alpha_2 \rho}{1 - L} + (n + 1)\beta_2 (\lambda - 1)\right\}.$$

Applying the latter estimate for $n = n_1 - 1$, one has

$$\bar{y} \le y_{n_1} \le y_0 \exp\left\{\frac{\alpha_2 \rho}{1-L} + n_1 \beta_2 (\lambda - 1)\right\}.$$

Thus,

$$n_1 \ge \frac{(1-L)\ln(\bar{y}/y_0) - \alpha_2\rho}{\beta_2(1-L)(\lambda-1)} \ge \frac{(1-L)\ln(\bar{y}/Y_2) - \alpha_2\rho}{\beta_2(1-L)(\lambda-1)}.$$
(5.24)

It follows the inequality (5.23) that $n_1 > \frac{\ln(\gamma(\lambda-1)/\rho)}{\ln L}$; in particular, $x_{n_1} < \rho e^{n_1 \ln L} \le \gamma(\lambda-1)$.

Next we show that, for $n_1 \leq n \leq n_0$, $x_n < \gamma(\lambda - 1) < \gamma \delta < \rho$; in particular, $x_{n_0} < \rho$, which will contradict to the choice n_0 . Suppose this is not true. Then there exists $n_1 < n_* \leq n_0$ such that $x_{n_*} \geq \gamma(\lambda - 1)$ and $x_n < \gamma(\lambda - 1)$ for all $n_1 \leq n < n_*$. For $n_1 \leq n < n_*$, by (5.19), we have

$$\begin{aligned} x_{n+1} &= F(x_n, y_n; \lambda) \le (1 + ax_n + b(\lambda - 1)) \, x_n \\ &\le (1 + (\gamma a + b)(\lambda - 1)) \, x_n \le (1 + (\gamma a + b)(\lambda - 1))^{n+1-n_1} x_{n_1}. \end{aligned}$$

Applying the estimate for $n = n_* - 1$, one gets

$$\gamma(\lambda - 1) \le x_{n_*} \le (1 + (\gamma a + b)(\lambda - 1))^{n_* - n_1} x_{n_1}$$

Thus

$$n_* \ge \frac{\ln(\gamma(\lambda - 1)/\rho) - n_1 \ln L}{\ln(1 + (\gamma a + b)(\lambda - 1))} + n_1.$$
(5.25)

By (5.18), for $n_1 \leq n < n_*$, we obtain

$$y_{n+1} = G(x_n, y_n; \lambda) \ge y_n(1 - \alpha_1 x_n + \beta_1(\lambda - 1))$$

$$\ge y_n(1 - \gamma \alpha_1(\lambda - 1) + \beta_1(\lambda - 1))$$

$$\ge y_n\left(1 + \frac{\beta_1}{2}(\lambda - 1)\right) \ge y_{n_1}\left(1 + \frac{\beta_1}{2}(\lambda - 1)\right)^{n+1-n_1}$$

Applying this for $n = n_* - 1$, one has

$$y^* \ge y_{n_*} \ge \bar{y} \left(1 + \frac{\beta_1}{2} (\lambda - 1) \right)^{n_* - n_1},$$

and hence

$$n_* \le \frac{\ln(y^*/\bar{y})}{\ln(1+\beta_1(\lambda-1)/2)} + n_1.$$
(5.26)

By using $1 + (\gamma a + b)\delta < L^{-1}$, inequality (5.25) implies

$$n_* \ge -\frac{\ln(\gamma(\lambda - 1)/\rho)}{\ln L} + 2n_1$$

and hence by (5.26),

$$n_1 \le \frac{\ln(\gamma(\lambda - 1)/\rho)}{\ln L} + \frac{\ln(y^*/\bar{y})}{\ln(1 + \beta_1(\lambda - 1)/2)}.$$

Furthermore, by (5.24), we get

$$\frac{(1-L)\ln(\bar{y}/Y_2) - \alpha_2\rho}{\beta_2(1-L)} \le \frac{(\lambda-1)\ln(\gamma(\lambda-1)/\rho)}{\ln L} + \frac{(\lambda-1)\ln(y^*/\bar{y})}{\ln(1+\beta_1(\lambda-1)/2)}$$

It contradicts to the inequality (5.23). This gives the existence of $M(\lambda)$.

The contradiction for both cases yields the existence of $M(\lambda)$ and hence we have finished the proof of (i).

(ii) To show the existence of $J(\lambda)$, we proceed in a similar way as that for $M(\lambda)$. First, note that the conclusion of (i) implies that there exists a unique integer $n_1 \leq M(\lambda)$ such that $y_{n_1} > \bar{y}$ and $y_n < \bar{y}$ and $x_n < \rho$ for $0 \leq n < n_1$. The above argument in (i) also shows that $x_n < \gamma(\lambda - 1)$ for $n_1 \leq n \leq M(\lambda)$. Next, let n^* be the integer such that $M(\lambda) < n^*$, $x_{n^*} \geq \gamma(\lambda - 1)$ and $x_n < \gamma(\lambda - 1)$ for all $M(\lambda) \leq n < n^*$. It suffices to show that $y_n > Y_3$ for some $n < n^*$. Suppose, on the contrary, that $y_n \leq Y_3$ for all $n < n^*$. As estimated in (i), we have that for $n_1 \leq n < M(\lambda)$, $Y_1 \leq y_n \leq y^*$, and hence by (5.19),

$$x_{n+1} = F(x_n, y_n; \lambda) \le (1 + ax_n + b(\lambda - 1))x_n$$

$$\le (1 + (\gamma a + b)(\lambda - 1))x_n \le (1 + (\gamma a + b)(\lambda - 1))^{n+1-n_1}x_{n_1};$$

in particular, $x_{M(\lambda)} \leq (1 + (\gamma a + b)(\lambda - 1))^{M(\lambda) - n_1} x_{n_1}$. Similarly, we have that for $M(\lambda) \leq n < n^*$, we have $Y_2 \leq y_n \leq Y_3$ and hence by (5.20),

$$\begin{aligned} x_{n+1} &= F(x_n, y_n; \lambda) = F_x(\bar{x}_n, y_n; \lambda) x_n \le L^{-1} x_n \\ &\le L^{M(\lambda) - n - 1} x_{M(\lambda)} \le L^{M(\lambda) - n - 1} (1 + (\gamma a + b)(\lambda - 1))^{M(\lambda) - n_1} x_{n_1}. \end{aligned}$$

Applying the estimate for $n = n^* - 1$, we get

$$\gamma(\lambda - 1) \le x_{n^*} \le L^{M(\lambda) - n^*} (1 + (\gamma a + b)(\lambda - 1))^{M(\lambda) - n_1} x_{n_1}.$$

Note that $x_{n_1} \leq \rho L^{n_1}$ and $1 + (\gamma a + b)(\lambda - 1)) \leq L^{-1}$. Thus

$$n^* \ge 2n_1 - \frac{\ln(\gamma(\lambda - 1)/\rho)}{\ln L}.$$
 (5.27)

By (5.18), for $M(\lambda) \le n < n^*$,

$$y_{n+1} = G(x_n, y_n; \lambda) \ge y_n (1 - \alpha_1 x_n + \beta_1 (\lambda - 1))$$

$$\ge y_n (1 - \gamma \alpha_1 (\lambda - 1) + \beta_1 (\lambda - 1))$$

$$\ge y_n \left(1 + \frac{\beta_1}{2} (\lambda - 1) \right) \ge y_{M(\lambda)} \left(1 + \frac{\beta_1}{2} (\lambda - 1) \right)^{n+1-M(\lambda)}.$$

Applying the estimate for $n = n^* - 2$, we obtain

$$Y_3 \ge y_{n^*-1} \ge y^* \left(1 + \frac{\beta_1}{2}(\lambda - 1)\right)^{n^* - 1 - M(\lambda)}$$

and

$$n^* - 1 \le M(\lambda) + \frac{\ln(Y_3/y^*)}{\ln(1 + \beta_1(\lambda - 1)/2)}.$$
(5.28)

Combining (5.27) and (5.28), we get,

$$2n_1 \le M(\lambda) + 1 + \frac{\ln(\gamma(\lambda - 1)/\rho)}{\ln L} + \frac{\ln(Y_3/y^*)}{\ln(1 + \beta_1(\lambda - 1)/2)}$$

Note that inequality (5.26) holds with n_* replaced by $M(\lambda)$. The above inequality then implies

$$n_1 \le \frac{\ln(\gamma(\lambda - 1)/\rho)}{\ln L} + \frac{\ln(Y_3/\bar{y})}{\ln(1 + \beta_1(\lambda - 1)/2)} + 1,$$

which contradicts to (5.24) and (5.23). This completes the proof of (ii).

(iii) We first prove the estimate of x_n for $0 \le n \le M(\lambda)$. Let n_1 be as before. Then $x_n \le x_0 e^{n \ln L}$ for $0 \le n \le n_1$. Note that inequality (5.26) holds with n_* replaced by $M(\lambda)$; that is,

$$M(\lambda) \le \frac{\ln(y^*/\bar{y})}{\ln(1+\beta_1(\lambda-1)/2)} + n_1$$

This inequality together with (5.24) gives

$$\frac{n_1}{M(\lambda) - n_1} \ge \frac{\left[(1 - L)\ln(\bar{y}/Y_2) - \alpha_2\rho\right]\ln(1 + \beta_1(\lambda - 1)/2)}{\beta_2(1 - L)(\lambda - 1)\ln(y^*/\bar{y})}.$$
(5.29)

By (5.23), there exists a constant K > 1 independent of λ such that the right hand side of inequality (5.29) is greater K. Therefore, for $n_1 \leq n \leq M(\lambda)$,

$$n_1 \ge \frac{K}{1+K}M(\lambda) \ge \frac{(1+C_0)M(\lambda)}{2} \ge \frac{(1+C_0)n}{2},$$

where $C_0 = 2K/(1+K) - 1 > 0$, and hence,

$$x_{n+1} \le (1 + (\gamma a + b)(\lambda - 1))^{n+1-n_1} x_{n_1}$$

$$\le x_0 \exp\{(n+1-n_1)\ln(1 + (\gamma a + b)(\lambda - 1)) + n_1\ln L\}$$

$$< x_0 \exp\{(2n_1 - n - 1)\ln L\} < x_0 e^{C_0 n \ln L}.$$

Finally, we take $C \ge \min\{-C_0 \ln L, -\ln L\}$. Then C > 0 and $x_n \le x_0 e^{-Cn}$ for $0 \le n \le M(\lambda)$. Note that the constant C is independent of λ and (x_0, y_0) . The estimate of x_n for $M(\lambda) \le n \le J(\lambda)$ can be obtained by the similar arguments applied to the reversed system.

We are in position to state the delay of stability loss for general discrete dynamical systems.

Theorem 5.2. Assume that for system (5.13) the hypotheses **(H1)-(H4)** are satisfied. Then

(i) for any fixed Y_1 , Y_2 and ℓ with $Y_1 < Y_2 < y^*$ and $0 < \ell < 1$, there exist $\rho > 0$ and $\delta > 0$ such that if (x_0, y_0) is an initial point with $\ell \rho < x_0 < \rho$, $y_0 < y^*$ and $Y_1 < S(x_0, y_0) < Y_2$, then, for $1 < \lambda < 1 + \delta$, there exists a unique integer $N(\lambda) > 0$ such that $x_n < \rho \le x_{N(\lambda)}$ for $0 \le n < N(\lambda)$ and $y_{N(\lambda)} > y^*$; (ii) for the above $N(\lambda)$, one has that $U(x_{N(\lambda)}, y_{N(\lambda)}) \to P(S(x_0, y_0))$ as $\lambda \to 1^+$ and, moreover, the convergence is uniform for the set of initial points (x_0, y_0) satisfying the above condition.

Proof. First, we pick $Y_4 > y^*$ and let ρ_0, δ_0, Y_3 and \bar{y} as in Lemma 5.1; in fact, Y_3 can be chosen so that $Y_3 < P(y_0)$. By a change of variables, we may assume that for system (5.13) with $\lambda = 1$, the local stable manifold of (0, y) for $y \in [Y_1, (Y_2 + y^*)/2]$ is given by

$$W^{s}(0, y) = \{(u, v) : v = y, 0 \le u \le \rho_1\}$$

and the local unstable manifold of (0, y) for $y \in [(y^* + Y_3)/2, Y_4]$ is given by

$$W^{u}(0, y) = \{(u, v) : v = y, 0 \le u \le \rho_1\},\$$

for some $\rho_1 > 0$. Then for $0 \le x \le \rho_1$, we have G(x, y; 1) = G(0, y; 1), S(x, y) = yfor $y \in [Y_1, (Y_2 + y^*)/2]$, U(x, y) = y for $y \in [(y^* + Y_3)/2, Y_4]$, $S(x_0, y_0) = y_0$, and $G(x, y; \lambda) = G(x, y; 1) + G_\lambda(x, y; \overline{\lambda})(\lambda - 1)$

$$\begin{aligned} f(x,y;\lambda) &= G(x,y;1) + G_{\lambda}(x,y;\lambda)(\lambda-1) \\ &= y + (G_{\lambda}(0,y;1) + O(x) + O(\lambda-1))(\lambda-1), \end{aligned} (5.30)$$

for $y \in [Y_1, (Y_2+y^*)/2] \cup [(y^*+Y_3)/2, Y_4]$. Moreover, since $G_{\lambda}(0, y; 1) > 0$, by (5.30), there exist $0 < \rho_2 < \rho_1$ and $\delta_1 > 0$ both small and A > 0 such that if $0 \le x < \rho_2$, $1 < \lambda < 1 + \delta_1$ and $y \in [Y_1, (Y_2+y^*)/2] \cup [(y^*+Y_3)/2, Y_4]$, then

$$G(x, y; \lambda) \ge y + A(\lambda - 1). \tag{5.31}$$

From now on, let $0 < \rho \leq \min\{\rho_0, \rho_2\}$ and $0 < \delta \leq \min\{\delta_0, \delta_1\}$ be small as in Lemma 5.1.

To establish statement (i), we will prove the existence of $N(\lambda)$ by contradiction. Suppose, on the contrary, that there exists a sequence $\{\lambda_m\}_{m=1}^{\infty}$ of numbers such that $1 < \lambda_m < 1 + \delta$, $\lambda_m \to 1$ as $m \to \infty$, and $x_n(\lambda_m) < \rho$ for all $n \ge 0$. For each λ_m , let $J(\lambda_m)$ and $M(\lambda_m)$ as in Lemma 5.1.

Let $Y \in (P(y_0), Y_4) \subset (Y_3, Y_4)$. We show that there exists a unique integer $L(\lambda_m)$ such that $y_{L(\lambda_m)+1} > Y$ and $y_n \leq Y$ for $0 \leq n \leq L(\lambda_m)$. Indeed, it is clear if $y_{J(\lambda_m)} > Y$; on the other hand, if $y_{J(\lambda_m)} \leq Y$ and $y_n \leq Y$ for $n \geq 0$, then for all $n \geq J(\lambda_m)$, we have $Y_3 \leq y_n \leq Y$ and hence by (5.31),

$$y_{n+1} = G(x_n, y_n; \lambda_m) \ge y_n + A(\lambda_m - 1)$$

$$\ge y_{J(\lambda_m)} + (n - J(\lambda_m) + 1)A(\lambda_m - 1) \to +\infty,$$

as $n \to +\infty$, which leads a contradiction. Then, while replacing $J(\lambda_m)$ by $L(\lambda_m)$, the estimates (iii) in Lemma 5.1 hold, that is, $x_n \leq \rho e^{-Cn}$ for $0 \leq n \leq M(\lambda_m)$ and $x_n \leq \rho e^{-C(L(\lambda_m)-n)}$ for $M(\lambda_m) \leq n \leq L(\lambda_m)$; in particular, the summation $\sum_{j=0}^{L(\lambda_m)} O(x_j)$ is bounded uniformly in m. By the hypothesis **(H3)** and the mean value theorem, one gets that for $n \geq 0$,

$$y_{n+1} = G(x_n, y_n; \lambda_m) = y_n + O(x_n) + G_{\lambda_m}(0, y_n; \bar{\lambda}_m)(\lambda_m - 1)$$

= \dots = y_0 + \sum_{j=0}^n O(x_j) + O(n(\lambda_m - 1)).

Applying the estimate for $n = L(\lambda_m) - 1$, we have $Y \ge y_{L(\lambda_m)} = y_0 + \sum_{j=0}^{L(\lambda_m)} O(x_j) + O(L(\lambda_m)(\lambda_m - 1))$, and hence $L(\lambda_m) = O((\lambda_m - 1)^{-1})$.

Note that the above proof for $L(\lambda_m) = O((\lambda_m - 1)^{-1})$ can be used to show that $L(\lambda_m) - n_3 = O((\lambda_m - 1)^{-1})$ where n_3 satisfies $y_{n_3} \leq (y^* + Y_3)/2 < y_{n_3+1}$.

Thus, by (iii) of Lemma 5.1, there exists $C_1 > 0$ such that for all sufficiently large $m, 0 \leq x_j \leq \rho e^{-C_1/(\lambda_m - 1)}$ provided $y_j \in (y^*, (y^* + Y_3)/2)$. Similarly, there exists $C_2 > 0$ such that for all sufficiently large $m, 0 \leq x_j \leq \rho e^{-C_2/(\lambda_m - 1)}$ provided $y_j \in ((Y_2 + y^*)/2, y^*)$. By (5.17), we get that for all sufficiently large m and for $y_j \in ((Y_2 + y^*)/2, (Y_3 + y^*)/2]$,

$$y_{j+1} = G(x_j, y_j; \lambda_m)$$

= $y_j + G_x(\bar{x}_j, y_j; \bar{\lambda}_m) x_j + G_{\lambda_m}(\bar{x}_j, y_j; \bar{\lambda}_m) (\lambda_m - 1)$
 $\geq y_j - |G_x| \rho e^{-C/(\lambda_m - 1)} + (G_{\lambda_m}(0, y_j; 1) + O(x_j) + O(\lambda_m - 1)) (\lambda_m - 1)$
 $\geq y_j + (G_{\lambda_m}(0, y_j; 1) + O(x_j) + O(\lambda_m - 1)) (\lambda_m - 1)$
 $> y_j,$

where $C = \min\{C_1, C_2\}$, for the second inequality, we replace $G_x \rho e^{-C/(\lambda_m - 1)}$ by $O(\lambda_m - 1)(\lambda_m - 1)$ and collect it into the coefficient of $\lambda_m - 1$, and for the last inequality, we use the assumption $G_{\lambda}(0, y; 1) > 0$ in the hypotheses **(H3)**. On the other hand, by (5.31), we have that for sufficiently large m and for $y_j \in [Y_1, (Y_2 + y^*)/2] \cup [(y^* + Y_3)/2, Y_4]$,

$$y_{j+1} = G(x_j, y_j; \lambda_m) = y_j + A(\lambda_m - 1) > y_j.$$

Therefore, for all sufficiently large m and for $y_i \in [Y_1, Y_4]$, we have $y_{j+1} - y_j > 0$ and $y_{j+1} \to y_j$ as $m \to \infty$.

By the hypotheses (H1) and (H2), one gets that

$$x_{n+1} = F(x_n, y_n; \lambda_m) = F_x(\bar{x}_n, y_n; \lambda_m) x_n$$

= $(1 + \epsilon_n + O(\lambda_m - 1)) F_x(0, y_n; 1) x_n$
= $\cdots = \prod_{j=0}^n (1 + \epsilon_j + O(\lambda_m - 1)) \prod_{j=0}^n F_x(0, y_j; 1) x_0,$ (5.32)

where $|\epsilon_n| = O(x_n) = O(e^{-Cn})$ for $0 \le n \le M(\lambda_m)$ and $|\epsilon_n| = O(x_n) = O(e^{-C(L(\lambda_m)-n)})$ for $M(\lambda_m) \le n \le L(\lambda_m)$. We show that the product $\prod_{j=0}^{L(\lambda_m)} (1 + \epsilon_j + O(\lambda_m - 1))$ is bounded away from zero and infinity uniformly in m. Indeed, since

$$\ln \prod_{j=0}^{L(\lambda_m)} (1 + \epsilon_j + O(\lambda_m - 1)) = \sum_{j=0}^{L(\lambda_m)} \ln(1 + \epsilon_j + O(\lambda_m - 1)),$$

and $x/2 \le \ln(1+x) \le x$ for x near zero, there exist numbers $d_1 \le d_2$ such that for all sufficiently large m,

$$\ln \prod_{j=0}^{L(\lambda_m)} (1+\epsilon_j + O(\lambda_m - 1)) \ge \sum_{j=0}^{L(\lambda_m)} \frac{\epsilon_j + O(\lambda_m - 1)}{2}$$
$$\ge \sum_{j=0}^{L(\lambda_m)} \epsilon_j / 2 + L(\lambda_m) O(\lambda_m - 1) \ge d_1$$

and

$$\ln \prod_{j=0}^{L(\lambda_m)} (1 + \epsilon_j + O(\lambda_m - 1)) \le \sum_{j=0}^{L(\lambda_m)} (\epsilon_j + O(\lambda_m - 1))$$
$$\le \sum_{j=0}^{L(\lambda_m)} \epsilon_j + L(\lambda_m)O(\lambda_m - 1) \le d_2$$

By (5.32) with $n = L(\lambda_m)$, one obtains that

$$\rho > x_{L(\lambda_m)+1} = \prod_{j=0}^{L(\lambda_m)} (1 + \epsilon_j + O(\lambda_m - 1)) \prod_{j=0}^{L(\lambda_m)} F_x(0, y_j; 1) x_0.$$
(5.33)

Dividing by ρ and taking the natural logarithm on both sides (noting that $x_0 > \ell \rho$) of (5.33), we get that for sufficiently large m,

$$0 > \ln \prod_{j=0}^{L(\lambda_m)} F_x(0, y_j; 1) + \ln \ell + d_1 = \sum_{j=0}^{L(\lambda_m)} \ln F_x(0, y_j; 1) + \ln \ell + d_1$$

$$= \sum_{j=0}^{L(\lambda_m)} \frac{\ln F_x(0, y_j; 1)}{y_{j+1} - y_j} (y_{j+1} - y_j) + \ln \ell + d_1$$

$$= \sum_{j=0}^{L(\lambda_m)} \frac{\ln F_x(0, y_j; 1)(y_{j+1} - y_j)}{(G_\lambda(0, y_j; 1) + O(x_j) + O(\lambda_m - 1))(\lambda_m - 1)} + \ln \ell + d_1$$
(5.34)

$$= \frac{1}{\lambda_m - 1} \sum_{j=0}^{L(\lambda_m)} \frac{\ln F_x(0, y_j; 1)}{G_\lambda(0, y_j; 1)} (y_{j+1} - y_j)$$

$$+ \frac{1}{\lambda_m - 1} \sum_{j=0}^{L(\lambda_m)} (O(x_j) + O(\lambda_m - 1))(y_{j+1} - y_j) + \ln \ell + d_1,$$

where the last equality holds because that the mean value theorem implies $\frac{u}{v+z} = \frac{u}{v} + O(z)$ if $v \neq 0$. Note that, as $m \to \infty$, the summation

$$\sum_{j=0}^{L(\lambda_m)} \frac{\ln F_x(0, y_j; 1)}{G_\lambda(0, y_j; 1)} (y_{j+1} - y_j)$$

is a Riemann sum of the integral

$$\int_{y_0}^{Y} \frac{\ln F_x(0, y; 1)}{G_\lambda(0, y; 1)} \, dy,$$

and

$$\sum_{j=0}^{L(\lambda_m)} (O(x_j) + O(\lambda_m - 1))(y_{j+1} - y_j)$$

$$\leq \Delta y \sum_{j=0}^{L(\lambda_m)} O(x_j) + O(\lambda_m - 1)(Y - y_0) \to 0$$

as $m \to \infty$, where $\Delta y = \max\{|y_{j+1} - y_j| : 0 \le j \le L(\lambda_m)\}$. Now multiplying $(\lambda_m - 1)$ on both sides of (5.34) and taking the limit as $m \to \infty$, we get

$$0 \ge \int_{y_0}^Y \frac{\ln F_x(0,y;1)}{G_\lambda(0,y;1)} \, dy > \int_{y_0}^{P(y_0)} \frac{\ln F_x(0,y;1)}{G_\lambda(0,y;1)} \, dy = 0.$$

The contradiction gives the existence of $N(\lambda)$. The uniqueness of $N(\lambda)$ follows from its definition.

Next, we establish statement (ii). We will first show the existence of the limit. Note that the proof of (i) also shows that for any $Y > P(y_0)$, if λ is sufficiently close to 1 then $y_{N(\lambda)} < Y$. From Lemma 5.1, if λ is sufficiently close to 1 then $y_{N(\lambda)} > Y_3$. It remains to show that for any $Y_3 < Y < P(y_0)$, if λ is sufficiently close to 1, then $y_{N(\lambda)} > Y$. We prove this again by contradiction. Thus, let $Y_3 < Y < P(y_0)$ and suppose that for any m, there exists $1 < \lambda_m < 1 + \delta$ such that $\lambda_m \to 1$ as $m \to \infty$ and $y_n \leq Y$ for all $0 \leq n \leq N(\lambda_m)$. Repeating the procedure for the proof of (i), similar to (5.33) we now have

$$\rho < x_{N(\lambda_m)+1} = \prod_{j=0}^{N(\lambda_m)} (1 + \epsilon_j + O(\lambda_m - 1)) \prod_{j=0}^{N(\lambda_m)} F_x(0, y_j; 1) x_0.$$
(5.35)

Let d_2 as in the proof of (i). As before, we divide by ρ and take the natural logarithm on both sides of (5.35) to get that for all sufficiently large m,

$$0 < \ln \prod_{j=0}^{N(\lambda_m)} F_x(0, y_j; 1) + d_2 = \sum_{j=0}^{N(\lambda_m)} \ln F_x(0, y_j; 1) + d_2$$

= $\sum_{j=0}^{N(\lambda_m)} \frac{\ln F_x(0, y_j; 1)}{y_{j+1} - y_j} (y_{j+1} - y_j) + d_2$
= $\sum_{j=0}^{N(\lambda_m)} \frac{\ln F_x(0, y_j; 1)(y_{j+1} - y_j)}{(G_\lambda(0, y_j; 1) + O(x_j) + O(\lambda_m - 1))(\lambda_m - 1)} + d_2$
= $\frac{1}{\lambda_m - 1} \sum_{j=0}^{N(\lambda_m)} \frac{\ln F_x(0, y_j; 1)}{G_\lambda(0, y_j; 1)} (y_{j+1} - y_j)$
+ $\frac{1}{\lambda_m - 1} \sum_{j=0}^{N(\lambda_m)} (O(x_j) + O(\lambda_m - 1))(y_{j+1} - y_j) + d_2.$

Multiplying $(\lambda_m - 1)$ on both sides and taking the limit as $m \to \infty$, one gets that

$$0 \le \int_{y_0}^{Y} \frac{\ln F_x(0,y;1)}{G_\lambda(0,y;1)} \, dy < \int_{0}^{P(y_0)} \frac{\ln F_x(0,y;1)}{G_\lambda(0,y;1)} \, dy = 0.$$

The contradiction yields the existence of limit.

To show the uniformity, we prove by contradiction. Suppose, on the contrary, that there exist $\epsilon_0 > 0$, $\lambda_m \to 1^+$ as $m \to \infty$ and (x_0^m, y_0^m) with $l\rho < x_0^m < \rho$, $y_0^m < y^*$ and $Y_1 < S(x_0^m, y_0^m) < Y_2$ so that $|y_{N(\lambda_m)}^m - P(y_0^m)| \ge \epsilon_0$ for all m. Without loss of generality, we assume that $y_{N(\lambda_m)-1}^m \ge P(y_0^m) + \epsilon_0$ for $m \ge M$, where $M \in \mathbb{N}$ is a constant. Hence

$$\int_{y_0^m}^{y_{N(\lambda_m)-1}^m} \frac{\ln F_x(0,y;1)}{G_\lambda(0,y;1)} \, dy - \int_{y_0^m}^{P(y_0^m)} \frac{\ln F_x(0,y;1)}{G_\lambda(0,y;1)} \, dy > K_0 \epsilon_0,$$

or equivalently,

$$\int_{y_0^m}^{y_{N(\lambda_m)-1}^m} \frac{\ln F_x(0,y;1)}{G_\lambda(0,y;1)} \, dy > K_0 \epsilon_0$$

for some constant $K_0 > 0$ and all $m \ge M$.

On the other hand, for m large, from (33) we have

$$\rho > x_{N(\lambda_m)-1}^m = \sum_{j=0}^{N(\lambda_m)-2} (1+\epsilon_j + O(\lambda_m-1) \prod_{j=0}^{N(\lambda_m)-2} F_x(0, y_j^m; 1) x_0^m.$$

Since $x_0^m > l\rho$, after dividing by ρ and taking logarithm, we get as (5.34) that for m large,

$$0 > \frac{1}{\lambda_m - 1} \sum_{j=0}^{N(\lambda_m) - 2} \frac{\ln F_x(0, y_j^m; 1)}{G_\lambda(0, y_j^m; 1)} (y_{j+1}^m - y_j^m) + \frac{1}{\lambda_m - 1} \sum_{j=0}^{N(\lambda_m) - 2} (O(x_j^m) + O(\lambda_m - 1))(y_{j+1}^m - y_j^m) + \ln l + d_1.$$

Therefore,

$$\sum_{j=0}^{N(\lambda_m)-2} \frac{\ln F_x(0, y_j^m; 1)}{G_\lambda(0, y_j^m; 1)} (y_{j+1}^m - y_j^m) < \sum_{j=0}^{N(\lambda_m)-2} (O(x_j^m) + O(\lambda_m - 1))(y_{j+1}^m - y_j^m) - (\lambda_m - 1)(\ln l + d_1) < \Delta^m y(K_1 + O(\lambda_m - 1)) - (\lambda_m - 1)(\ln l + d_1),$$

where K_1 is a constant independent of (x_0^m, y_0^m) and $\Delta^m y = \max\{y_{j+1}^m - y_j^m\}$, which approaches zero as $m \to \infty$.

By the mean value theorem, there exists $y_j^* \in [y_j^m, y_{j+1}^m]$ for each i such that

$$\int_{y_0^m}^{y_{N(\lambda)-1}^m} \frac{\ln F_x(0,y;1)}{G_\lambda(0,y;1)} \, dy = \sum_{j=0}^{N(\lambda_m)-2} \frac{\ln F_x(0,y_j^*;1)}{G_\lambda(0,y_j^*;1)} (y_{j+1}^m - y_j^m).$$

Hence

$$|\sum_{j=0}^{N(\lambda_m)-2} \frac{\ln F_x(0, y_j^m; 1)}{G_\lambda(0, y_j^m; 1)} (y_{j+1}^m - y_j^m) - \int_{y_0^m}^{y_{N(\lambda)-1}^m} \frac{\ln F_x(0, y; 1)}{G_\lambda(0, y; 1)} \, dy|$$

= $|\sum_{j=0}^{N(\lambda_m)-2} \left(\frac{\ln F_x(0, y_j^m; 1)}{G_\lambda(0, y_j^m; 1)} - \frac{\ln F_x(0, y_j^*; 1)}{G_\lambda(0, y_j^*; 1)} \right) (y_{j+1}^m - y_j^m)$
 $\leq K\Delta^m y \sum_{j=0}^{N(\lambda_m)-2} (y_{j+1}^m - y_j^m) \leq K\Delta^m y (Y_4 - Y_1),$

where

$$K = \max\left\{ \left| \frac{d}{dy} \frac{\ln F_x(0, y; 1)}{G_\lambda(0, y; 1)} \right| : y \in [Y_1, Y_4] \right\}.$$

We now have, for m large,

$$\begin{split} &\int_{y_0^m}^{y_{N(\lambda)-1}} \frac{\ln F_x(0,y;1)}{G_\lambda(0,y;1)} \, dy \\ &\leq \sum_{j=0}^{N(\lambda_m)-2} \frac{\ln F_x(0,y_j^m;1)}{G_\lambda(0,y_j^m;1)} (y_{j+1}^m - y_j^m) + K\Delta^m y (Y_4 - Y_1) \\ &\leq \Delta^m y (K_1 + O(\lambda_m - 1)) - (\lambda_m - 1) (\ln l + d_1) + K\Delta^m y (Y_4 - Y_1). \end{split}$$

The latter approaches zero as $m \to \infty$. The contradiction gives the uniformity.

Next, we shall apply Theorem 5.2 to the Nicholson-Bailey model f_{λ} in (2.2). Let $F(x, y; \lambda) = y(1 - e^{-x})$ and $G(x, y; \lambda) = \lambda y e^{-x}$. Then the hypotheses **(H1)-(H3)** are satisfied with $y^* = 1$, $F_x(0, y; 1) = y$, and $G_{\lambda}(0, y; 1) = y$. Let P be as in (5.14), that is, for 0 < y < 1,

$$\int_{y}^{P(y)} \frac{\ln F_x(0,t;1)}{G_\lambda(0,t;1)} \, dt = \int_{y}^{P(y)} \frac{\ln t}{t} \, dt = 0,$$

and hence P(y) = 1/y and the hypothesis **(H4)** is satisfied. It is easy to see that, if y < 1 and $\tau(y)$ is defined as in Section 3 (i.e., $H(0, y) = H(0, \tau(y))$ where $H(x, y) = x + y - \ln y$ is the integral for $\lambda = 1$, see item 1 of Theorem 3.1), then $P(y) = 1/y > \tau(y)$. Together with Theorem 5.2, this will imply the following result about nonexistence of periodic points for the Nicholson-Bailey model f_{λ} with λ close to one.

Corollary 5.3. Let $1 < c_1 < c_2$ be any two numbers $(c_1$ being arbitrarily close to one and c_2 arbitrarily large) and let \widetilde{R}_1 (resp. \widetilde{R}_2) be the region bounded by the level curve $H(x,y) = c_1$ (resp. $H(x,y) = c_2$) and the y-axis. Then there exists $\widetilde{\lambda} > 1$ such that for $1 < \lambda < \widetilde{\lambda}$, any full orbit of f_{λ} which is contained in \widetilde{R}_2 , must be contained in fact in \widetilde{R}_1 ; in particular, f_{λ} has no periodic orbit that lies entirely in \widetilde{R}_2 and visits $\widetilde{R}_2 \setminus \widetilde{R}_1$ at least once.

Proof. Let \tilde{Y} (resp. \hat{Y}) be the point of intersection of the level curve $H(x, y) = c_2$ (resp. $H(x, y) = c_1$) with the y-axis below the line y = 1, and let Y_1, Y_2 be any (fixed) numbers such that $0 < Y_1 < \tilde{Y} < \tilde{Y} < Y_2 < 1$. Further, let \tilde{X} be the maximum value of the x-coordinate on the curve $H(x, y) = c_2$, i.e., $\tilde{X} = c_2 - 1$. By applying Theorem 5.2 for the numbers Y_1, Y_2 and $\ell := Y_1 e^{-\tilde{X}}$, we get ρ and δ satisfying the conclusions of Theorem 5.2.

Next, we choose $0 < \tilde{\rho} < \rho$ small enough so that the level curve $H(x, y) = Y_2 - \ln Y_2$ intersects the vertical line $x = \tilde{\rho}$ at two points (this is equivalent to the inequality $0 < \tilde{\rho} < Y_2 - \ln Y_2 - 1$) and, in addition, the following inequality holds

$$e^{-\tilde{\rho}} > \frac{1 + (y_{\tilde{\rho}}^+ - 1)/3}{1 + 2(y_{\tilde{\rho}}^+ - 1)/3}$$

where $y_{\tilde{\rho}}^+ > 1$ is the point of intersection of the level curve $H(x, y) = c_1$ with the vertical line $x = \tilde{\rho}$ (obviously, this inequality is satisfied for sufficiently small $\tilde{\rho}$). From now on, $\tilde{\rho}$ is fixed. Let us denote $R = closure(\tilde{R}_2 \setminus \tilde{R}_1), R_{\tilde{\rho}} = \{(x, y) \in R : x \geq \tilde{\rho}\}, R_{\ell}^- = \{(x, y) \in R : \ell \tilde{\rho} < x < \tilde{\rho}, y < 1\}$ and let R_{ℓ}^* be the open set

(open "quadrilaterial") below the line y = 1, which is bounded by two vertical lines $x = \ell \tilde{\rho}, x = \tilde{\rho}$ and two level curves $H(x, y) = Y_1 - \ln Y_1, H(x, y) = Y_2 - \ln Y_2$.

Obviously we can choose $\delta_1 > 0$ such that for $1 < \lambda < 1 + \delta_1$, the fixed point $(\bar{p}_{\lambda}, \bar{q}_{\lambda}) = (\ln \lambda, \lambda \ln \lambda / (\lambda - 1))$ of f_{λ} lies inside the region \tilde{R}_1 to the left from the vertical line $x = \tilde{\rho}$.

First we prove Claim 1. Any forward orbit of f_1 with initial point $(x_0, y_0) \in R_{\tilde{\rho}}$ must visit R_{ℓ}^- . Indeed, if one has $x_{n_0-1} \geq \tilde{\rho}$ and $x_{n_0} < \tilde{\rho}$ for some $n_0 > 0$, then

$$x_{n_0} = y_{n_0-1} \left(1 - e^{-x_{n_0-1}} \right) = y_{n_0-1} e^{-\bar{x}} x_{n_0-1},$$

where $\bar{x} \in (0, x_{n_0-1})$ is taken by the mean value theorem, and hence $x_{n_0} \geq Y_1 e^{-\tilde{X}} \tilde{\rho} = \ell \tilde{\rho}$. So given a point $(x_0, y_0) \in R_{\tilde{\rho}}$ we may define by Claim 1, $n_0 = n_0(x_0, y_0)$ as the minimal positive integer for which $f_1^{n_0}(x_0, y_0) \in R_{\ell}^-$.

We now prove Claim 2. For any $\epsilon > 0$ there exists $\delta_2 = \delta_2(\epsilon) > 0$ such that for every $(x, y) \in R_{\tilde{\rho}}$ there is a positive integer $\tilde{N} = \tilde{N}(x, y, \epsilon)$ such that for any $1 \leq \lambda < 1+\delta_2$ one has $|H(f_{\lambda}^{\tilde{N}}(x, y)) - H(f_1^{\tilde{N}}(x, y))| < \epsilon$ and $f_{\lambda}^{\tilde{N}}(x, y) \in R_{\ell}^*$. Indeed, by continuity of $f_{\lambda}(x, y)$ and H(x, y) in all of their variables, for every $(x_0, y_0) \in R_{\tilde{\rho}}$ there exist an open neighborhood $U = U(x_0, y_0)$ of (x_0, y_0) and $\delta_0 = \delta_0(x_0, y_0) > 0$ such that for all $(x, y) \in U$ and $1 \leq \lambda < 1 + \delta_0$, one has that

$$|H(f_{\lambda}^{n_0(x_0,y_0)}(x,y)) - H(f_1^{n_0(x_0,y_0)}(x_0,y_0))| < \epsilon/2$$

and $f_{\lambda}^{n_0(x_0,y_0)}(x,y) \in R_{\ell}^*$. The collection of the neighborhoods $U(x_0,y_0)$'s for all $(x_0,y_0) \in R_{\tilde{\rho}}$ is an open covering of $R_{\tilde{\rho}}$. By compactness of $R_{\tilde{\rho}}$, there exists a finite subcovering $U(x_i,y_i), i = 1, \ldots, m$. Now we take $\delta_2 = \min\{\delta_0(x_1,y_1), \ldots, \delta_0(x_m,y_m)\}$. Since every point $(x,y) \in R_{\tilde{\rho}}$ is contained in some $U(x_i,y_i)$ with $i \in \{1,\ldots,m\}$, we have that for any $1 \leq \lambda < 1 + \delta_2$,

$$|H(f_{\lambda}^{n_{0}(x_{i},y_{i})}(x,y)) - H(f_{1}^{n_{0}(x_{i},y_{i})}(x,y))|$$

$$\leq |H(f_{\lambda}^{n_{0}(x_{i},y_{i})}(x,y)) - H(f_{1}^{n_{0}(x_{i},y_{i})}(x_{i},y_{i}))|$$

$$+ |H((f_{1}^{n_{0}(x_{i},y_{i})}(x_{i},y_{i}) - H(f_{1}^{n_{0}(x_{i},y_{i})}(x,y))|$$

$$< \epsilon,$$

and so the claim is proved with $N = n_0(x_i, y_i)$.

Next we prove Claim 3. There exists $\delta_3 > 0$ such that for $1 < \lambda < 1 + \delta_3$ the following holds: if some full orbit of f_{λ} is contained entirely in \tilde{R}_2 and visits R at least once, then this orbit must visit R_{ℓ}^* . For this end we choose $0 < \delta_3 < \delta_1$ small enough so that if $1 < \lambda < 1 + \delta_3$ then $\bar{q}_{\lambda} < 1 + (y_{\tilde{\rho}}^+ - 1)/3$. To prove the claim, first notice that if the initial point (x_0, y_0) belongs to $R_{\tilde{\rho}}$ then the claim follows from Claim 2. So we may assume that (x_0, y_0) belongs to $R \setminus (R_{\tilde{\rho}} \bigcup R_{\ell}^*)$. Obviously, $x_0 \neq 0$, because otherwise the orbit of (x_0, y_0) would be unbounded. We consider two cases: (i) $y_0 > 1$; and (ii) $y_0 < 1$. For the first case consider forward iterates of (x_0, y_0) under f_{λ} with $1 < \lambda < 1 + \delta_3$. Then by using identity (4.5), we get that under consecutive forward iterates, the values of H increase unless the y-coordinate for the next iterate is smaller than \bar{q}_{λ} . Hence (with help of Theorem 4.4), there is a number n > 0 such that $(x_i, y_i) \in R$ with $x_i < \tilde{\rho}, y_i > 1$ for $i = 0, 1, \ldots, n - 1$ and either (subcase 1) $(x_n, y_n) \in R_{\tilde{\rho}}$, or (subcase 2) $y_n < \bar{q}_{\lambda}$. For subcase 1, we apply Claim 2 to get the result, while subcase 2 is impossible: indeed, otherwise

one would have

$$y_n = \lambda y_{n-1} e^{-x_{n-1}} > 1 \cdot y_{\tilde{\rho}}^+ e^{-\tilde{\rho}} > y_{\tilde{\rho}}^+ \frac{1 + (y_{\tilde{\rho}}^+ - 1)/3}{1 + 2(y_{\tilde{\rho}}^+ - 1)/3} > 1 + (y_{\tilde{\rho}}^+ - 1)/3,$$

while $y_n < \bar{q}_{\lambda} < 1 + (y_{\tilde{\rho}}^+ - 1)/3$. For case (ii) we apply identity (4.5) to backward iterates of (x_0, y_0) and get the fact that (for any $\lambda > 1$), under consecutive backward iterates, the values of H increase unless the y-coordinates for these iterates are bigger than \bar{q}_{λ} . This implies that there is a number $n \ge 0$ such that $(x_{-i}, y_{-i}) \in R$ with $x_{-i} < \tilde{\rho}$ for $i = 0, 1, \ldots, n$ and either (subcase 1) $x_{-n} \ge \tilde{\rho}$ or (subcase 2) $(x_n, y_n) \in R, x_{-n} < \tilde{\rho}, y_{-n} > 1$. For subcase 2 we have the situation of case (i) and we are done (but in fact, subcase 2 is impossible by similar arguments as for subcase 2 of case (i)). For subcase 1, by applying the argument used in Claim 1 to f_{λ} with $\lambda > 1$, one gets that $x_{-(n-1)} > \ell \tilde{\rho}$ and so $(x_{-(n-1)}, y_{-(n-1)}) \in R_{\ell}^- \subset R_{\ell}^*$. Since $P(y) > \tau(y)$, we have

 $d := \min\{H(0, P(y)) - H(0, \tau(y)) : (0, y) \in \mathbb{R}, y < 1\} > 0.$

So by item (ii) of Theorem 5.2, we can choose $0 < \delta_4 < \delta$ such that for $1 < \lambda < 1 + \delta_4$ and for all $(x_0, y_0) \in R^*_{\ell}$ one has

$$H(x_{N(x_0,y_0,\lambda)}, y_{N(x_0,y_0,\lambda)}) - H(x_0,y_0) > 2d/3$$

(in Theorem 5.2, the number $N(x_0, y_0, \lambda)$ was denoted simply by $N(\lambda)$) and $(x_{N(x_0, y_0, \lambda)}, y_{N(x_0, y_0, \lambda)}) \in R_{\tilde{\rho}}$.

Finally we take $\tilde{\delta} = \min\{\delta_2(d/3), \delta_3, \delta_4\}$ and consider f_{λ} with $1 < \lambda < 1 + \tilde{\delta}$. To prove the corollary, suppose by the contrary that there is a full orbit of f_{λ} which is contained entirely in \tilde{R}_2 and for which $(x_0, y_0) \in R$. Then by Claim 3, we may assume without loss of generality that $(x_0, y_0) \in R_\ell^*$. Thus, by the choices of δ_2, δ_4 and since f_1 preserves the value of the level curve H, we have that the initial point $(x_0, y_0) \in R_\ell^-$ under $k := N(x_0, y_0, \lambda) + \tilde{N}(x_{N(x_0, y_0, \lambda)}, y_{N(x_0, y_0, \lambda)}, d/3)$ iterates of f_{λ} will raise the value of H by at least d/3, and besides, the resulting point (x_k, y_k) lies in R_ℓ^* (and, which is easily seen, in R_ℓ^-). So we can repeat the above procedure infinitely many times, which will lead to a contradiction because $H(x, y) \leq c_2$ for all $(x, y) \in \tilde{R}_2$. The proof of the corollary is complete.

So the result of Corollary 5.3 gives us an additional information comparing with Corollary 4.7 on nonexistence of periodic orbits. Note that the proof of Corollary 5.3 also implies that there is no invariant closed curve in \tilde{R}_2 that meets $\tilde{R}_2 \setminus \tilde{R}_1$.

Appendix: center of mass for orbits

So far, for the Nicholson-Bailey model f_{λ} with $\lambda > 1$, we do not know whether periodic points of period bigger than 3 exist or not on the whole region Q. In the case when a periodic cycle exists, we show that the fixed point $(\bar{p}_{\lambda}, \bar{q}_{\lambda}) = (\ln \lambda, \frac{\lambda \ln \lambda}{\lambda - 1})$ must be the center of mass of the cycle. Moreover, the Cesaro averages of orbits whose coordinates have less than exponential growths must tend to the fixed point $(\bar{p}_{\lambda}, \bar{q}_{\lambda})$.

Proposition 5.4. Let (x_n, y_n) be the nth iterate of $(x_0, y_0) \in Q$ under f_{λ} with $\lambda > 1$. Then the following statements hold:

1. If (x_0, y_0) is a period-k point for f_{λ} , then $\frac{1}{k} \sum_{n=0}^{k-1} x_n = \bar{p}_{\lambda}$ and $\frac{1}{k} \sum_{n=0}^{k-1} y_n = \bar{q}_{\lambda}$.

2. If $\lim_{k\to\infty} \frac{\ln y_k}{k} = 0$ then $\lim_{k\to\infty} \frac{1}{k} \sum_{n=0}^{k-1} x_n = \bar{p}_{\lambda}$. If, in addition, $\lim_{k\to\infty} \frac{y_k}{k} = 0$ then $\lim_{k\to\infty} \frac{1}{k} \sum_{n=0}^{k-1} y_n = \bar{q}_{\lambda}$.

Proof. By (2.2) and periodicity, we have $y_n = \lambda y_{n-1} e^{-x_{n-1}}$ for $n = 1, \dots, (k-1)$ and $y_0 = y_k = \lambda y_{k-1} e^{-x_{k-1}}$. Multiplying these relations, we get

$$\prod_{n=0}^{k-1} y_n = \lambda^k \cdot \left(\prod_{n=0}^{k-1} y_n\right) \cdot e^{-\sum_{n=0}^{k-1} x_n}.$$

Since $y_n \neq 0$ for n = 0, 1, ..., k - 1, we have $\frac{1}{k} \sum_{n=0}^{k-1} x_n = \ln \lambda = \bar{p}_{\lambda}$. By (2.3) and periodicity, we have $y_n = x_{n+1} + \frac{y_{n+1}}{\lambda}$ for n = 0, 1, ..., (k-2) and $y_{k-1} = x_k + \frac{y_k}{\lambda} = x_0 + \frac{y_0}{\lambda}$. The summation of these relations gives

$$\sum_{n=0}^{k-1} y_n = \sum_{n=0}^{k-1} x_n + \frac{1}{\lambda} \sum_{n=0}^{k-1} y_n.$$

Therefore, $\frac{1}{k} \sum_{n=0}^{k-1} y_n = \frac{\lambda \ln \lambda}{\lambda - 1} = \bar{q}_{\lambda}$. The proof of item 1 is complete.

For item 2, by proceeding in the same way as above, we get

$$\prod_{n=1}^{k} y_n = \lambda^k \cdot \left(\prod_{n=0}^{k-1} y_n\right) \cdot e^{-\sum_{n=0}^{k-1} x_n}.$$

Thus

$$\sum_{n=0}^{k-1} x_n = k \ln \lambda + \ln y_0 - \ln y_k.$$

Dividing the equality by k and letting $k \to \infty$, the hypothesis implies $\lim_{k\to\infty} \frac{1}{k} \sum_{n=0}^{k-1} x_n =$ \bar{p}_{λ} . The proof of the first statement is complete.

By (2.3) and the same argument as above, one gets

$$\sum_{n=0}^{k-1} y_n = \frac{\lambda}{\lambda - 1} \left(\sum_{n=1}^k x_n - \frac{y_0}{\lambda} + \frac{y_k}{\lambda} \right).$$

Again dividing the equality by k and letting $k \to \infty$, the hypothesis and the conclusion of the first statement applied to the initial point (x_1, y_1) imply the truth of the second statement.

REFERENCES

- [1] R. P. Agarwal, S. R. Grace, and D. O'Regan, Oscillation Theory for Difference and Functional Differential Equations, Kluwer Academic Publishers, London, 2000.
- [2] M. Balabane, M. Jazar, and P. Souplet, Oscillatory blow-up in nonlinear second order ODE's: the critical case, Discrete Contin. Dyn. Syst., 9 (2003), 577-584.
- [3] D. Bonheure, C. Fabry, and D. Smets, Periodic solutions of forced isochronous oscillators at resonance, Discrete Contin. Dyn. Syst., 8 (2002), 907-930.
- [4] H. N. Comins, M. P. Hassell, and R. M. May, The spatial dynamics of host-parasitoid systems, J. Animal Ecology 61 (1992), 735-748.
- [5] L. Edelstein-Keshet, Mathematical Models in Biology, 3rd ed., Random House/Birkhauser Mathematics Series, Random House, Inc., New York, 1988.
- [6] N. Fenichel, Persistence and smoothness of invariant manifolds for flows, Indiana Uni. Math. J. 21 (1971), 193-226.
- [7] M. Hirsch, C. Pugh, and M. Shub, Invariant Manifolds, Lect. Notes in Math. 583, Springer-Verlag, New York, 1976.
- [8] A. Katok and B. Hasselblatt, Introduction to the Modern Theory of Dynamical Systems, Cambridge University Press, Cambridge, 1995.

- W. Liu, Exchange Lemmas for singular perturbations with certain turning points, J. Differential Equations 167 (2000), 134-180.
- [10] R. Mané, Persistent manifolds are normally hyperbolic, Trans. Amer. Math. Soc. 246 (1977), 261-283.
- [11] R. M. May, Necessity and chance: deterministic chaos in ecology and evolution, Bull. Amer. Math. Soc. (N.S.) 32 (1995), 291–308.
- [12] C. Meier, W. Senn, R. Hauser, and M. Zimmermann, Strange limits of stability in hostparasitoid systems, J. Math. Biol. 32 (1994), 563–572.
- [13] E. F. Mishchenko, Yu. S. Koleso, A. Yu. Kolesov, and N. Kh. Rozo, Asymptotic Methods in Singularly Perturbed Systems, Monographs in Contemporary Mathematics, Consultants Bureau, New York, 1994.
- [14] J. D. Murray, Mathematical Biology I. An Introduction, Interdisciplinary Applied Mathematics, vol. 17, Springer-Verlag, New York, 2002.
- [15] A. J. Nicholson and V. A. Bailey, The balance of animal populations. Part I, Zool. Soc. (London), Porc. 3, 1935, pp. 551–598.
- [16] C. Robinson, Dynamical Systems: Stability, Symbolic Dynamics, and Chaos, 2nd ed., Studies in Advanced Mathematics, CRC Press, Boca Raton, FL, 1999.
- [17] S. Schecter, Persistent unstable equilibria and closed orbits of a singularly perturbed equation, J. Differential Equations 60 (1985), 131-141.
- [18] J. M. Smith, Models in Ecology, Cambridge University Press, Cambridge, 1974.
- [19] T.-C. Wei, Analysis of Nicholson-Bailey host-parasite model and its extension, Thesis, National Tsing Hua University, Hsinchu, Taiwan, June 1999.

Received September 2002; revised January 2003; final version June 2003.

- E-mail address: sbhsu@math.nthu.edu.tw
- *E-mail address*: mcli@math.ncue.edu.tw
- E-mail address: wliu@math.ukans.edu
- E-mail address: malkin@uic.nnov.ru