# On the $\lambda_{1}-$ and $\lambda_{2}$-Branching of Predator-Prey Equations Simulating an Immune Response 

Michio Kinoshita<br>Department of Mathematics, Shimane University, Matsue, Japan<br>(Received September 6, 1978)

This paper is concerned with the predator-prey equations simulating an immune response which G. I. Bell and G. H. Pimbley, Jr. studied. In [1], G. H. Pimbley, Jr. has shown that the $\boldsymbol{a}_{1}$-branching of the periodic solutions of this equations appears. In this paper, it will be shown that the $\lambda_{1}$ - and $\lambda_{2}$-branching appears under more restricted conditions.

## §1. Introduction

In this paper we are concerned with the $\lambda_{1}-$ and $\lambda_{2}$-branching of the following system

$$
\begin{align*}
& \frac{d u}{d s}=u\left[-\lambda_{2}-k \lambda_{2} u+k\left(\alpha_{2}-\lambda_{2}\right) v-\frac{k \alpha_{2}}{\theta} u v\right] \\
& \left.\frac{d v}{d s}=v\left[\lambda_{1}-k\left(\alpha_{1}-\lambda_{1}\right) u+k \lambda_{1}\right) u+k \lambda_{1} v\right] \tag{1}
\end{align*}
$$

where $\alpha_{1}>0, \alpha_{2}>0, \lambda_{1}>0, \lambda_{2}>0, \theta>0$ and $k>0$.
For the role of the variables $u, v$ and $s$, and the parameters $\alpha_{1}, \alpha_{2}, \lambda_{1}, \lambda_{2}, \theta$ and $k$, see [1].

Every point of intersection of the two curves

$$
\begin{align*}
& v=\frac{\lambda_{2}(1+k u)}{k\left(\alpha_{2}-\lambda_{2}-\frac{\alpha_{2}}{\theta} u\right)}  \tag{2a}\\
& v=\frac{1}{k \lambda_{1}}\left[-\lambda_{1}+k\left(\alpha_{1}-\lambda_{1}\right) u\right] \tag{2b}
\end{align*}
$$

is the singular point of the system. From equations (2), we can obtain that the vertical coordinates of the points of intersection of curves (2) satisfy the following quadratic equation

$$
\begin{equation*}
\frac{k \lambda_{1} \alpha_{2}}{\theta} v^{2}-\left[k\left(\alpha_{1}-\lambda_{1}\right)\left(\alpha_{2}-\lambda_{2}\right)-k \lambda_{1} \lambda_{2}-\frac{\lambda_{1} \alpha_{2}}{\theta}\right] v+\lambda_{2} \alpha_{1}=0 \tag{3}
\end{equation*}
$$

We will need the following condition;
(A) The two intersections of (2) exist in the set $A=\{(u, v) ; u \geqq 0, v \geqq 0\}$

We will need the following
Lemma. Fix the parameters $\alpha_{1}, \alpha_{2}, \lambda_{1}, \lambda_{2}$ and $k$ such that $\alpha_{1}>\lambda_{1}+\lambda_{2}, \alpha_{2}>\lambda_{1}$ $+\lambda_{2}$. There exists a value $\theta_{0}=\theta_{0}\left(\alpha_{1}, \alpha_{2}, \lambda_{1}, \lambda_{2}, k\right)$ such that if $\theta>\theta_{0}$, then assumption $(A)$ is satisfied for the parameters $\alpha_{1}, \alpha_{2}, \lambda_{1}, \lambda_{2}, \theta$ and $k$.

Proof. Let us consider the function $B=B\left(\alpha_{1}, \alpha_{2}, \lambda_{1}, \lambda_{2}, \theta, k\right)$ and $D=D\left(\alpha_{1}\right.$, $\left.\alpha_{2}, \lambda_{1}, \lambda_{2}, \theta, k\right)$ defined by

$$
\begin{align*}
& B\left(\alpha_{1}, \alpha_{2}, \lambda_{1}, \lambda_{2}, \theta, k\right)=k\left(\alpha_{1}-\lambda_{1}\right)\left(\alpha_{2}-\lambda_{2}\right)-k \lambda_{1} \lambda_{2}-\frac{\lambda_{1} \alpha_{2}}{\theta}  \tag{4}\\
& D\left(\alpha_{1}, \alpha_{2}, \lambda_{1}, \lambda_{2}, \theta, k\right)=B^{2}-\frac{4 k \alpha_{1} \alpha_{2} \lambda_{1} \lambda_{2}}{\theta} . \tag{5}
\end{align*}
$$

From that $B\left(\alpha_{1}, \alpha_{2}, \lambda_{1}, \lambda_{2}, \theta, k\right)$ and $D\left(\alpha_{1}, \alpha_{2}, \lambda_{1}, \lambda_{2}, \theta, k\right)$ are monotone increasing functions of $\theta$ and that $\alpha_{1}>\lambda_{1}$, we obtain this lemma.

Denote by $\left(u_{f}, v_{f}\right)$ the singular point that is the intersection of the two curves, of which vertical coordinates is smaller than the other. By solving (2), we have

$$
\begin{align*}
& v_{f}= \\
& \frac{k \theta\left(\alpha_{2}-\lambda_{2}\right)\left(\alpha_{1}-\lambda_{1}\right)-\alpha_{2} \lambda_{1}-k \theta \lambda_{1} \lambda_{2}-\sqrt{\left\{k \theta\left(\alpha_{2}-\lambda_{2}\right)-\alpha_{2} \lambda_{1}-k \theta \lambda_{1} \lambda_{2}\right\}^{2}-4 k \alpha_{1} \alpha_{2} \lambda_{1} \lambda_{2} \theta}}{2 k \alpha_{2} \lambda_{1}} . \tag{6}
\end{align*}
$$

For the system we define the function $F=F\left(\alpha_{1}, \alpha_{2}, \lambda_{1}, \lambda_{2}, \theta, k\right)$, by

$$
F\left(\alpha_{1}, \alpha_{2}, \lambda_{1}, \lambda_{2}, \theta, k\right)=u_{f} \lambda_{2}+\frac{\alpha_{2}}{\theta} u_{f} v_{f}-v_{f} \lambda_{1} .
$$

G. H. Pimbley, Jr. [1] proved

Thborem. Let condition $(\dot{A})$ be satisfied for all the parameters.
(i) If $F$ changes its signature from positive (negative) to negative (positive), then the branching of the periodic solutions which are asymptotically orbitally stable from the constant solution $\left(u_{f}, v_{f}\right)$ appear (vanish) at the zeros of $F$.
(ii) If $F$ changes its signature from positive to negative as one parameter is increased (decreased) with other parameters fixed, then the direction of the branching is towards higher (lower) values of the parameter; i.e. a right (left) branching with respect to the parameter.

Remark. For the more realistic model simulating an immune response, see [2].

## §2. $\lambda_{1}$ - and $\lambda_{2}$-branching

From (2a), we obtain

$$
\lambda_{2} u_{f}+\frac{\alpha_{2}}{\theta} u_{f} v_{f}=\left(\alpha_{2}-\lambda_{2}\right) v_{f}-\frac{\lambda_{2}}{k}
$$

Thus we have the following

$$
\begin{equation*}
\text { Lemma 1. } \quad F=\left(\alpha_{2}-\lambda_{2}-\lambda_{1}\right) v_{f}-\frac{\lambda_{2}}{k} . \tag{7}
\end{equation*}
$$

We will need the following
Lemma 2. Fix the parameters $\alpha_{1}, \alpha_{2}, \lambda_{2}$ and $k$ such that $\alpha_{1}>\alpha_{2}, \alpha_{2}>\lambda_{2}$. There exists a value $\theta_{1}=\theta_{1}\left(\alpha_{1}, \alpha_{2}, \lambda_{2}, k\right)$ such that if $\theta>\theta_{1}$, then condition $(A)$ is satisfied for every $\lambda_{1}$ such that $0<\lambda_{1}<\alpha_{2}-\lambda_{2}$.

Proof. Since $B\left(\alpha_{1}, \alpha_{2}, \lambda_{1}, \lambda_{2}, \theta, k\right)$ is a monotone decreasing function of $\lambda_{1}$ and $B\left(\alpha_{1}, \alpha_{2}, \alpha_{2}-\lambda_{2}, \lambda_{2}, \theta, k\right)=k\left(\alpha_{2}-\lambda_{2}\right)\left(\alpha_{1}-\alpha_{2}\right)-\frac{\left(\alpha_{2}-\lambda_{2}\right) \alpha_{2}}{\theta}$, we obtain the inequality $B\left(\alpha_{1}, \alpha_{2}, \lambda_{1}, \lambda_{2}, \theta, k\right)>k\left(\alpha_{2}-\lambda_{2}\right)\left(\alpha_{1}-\alpha_{2}\right)-\frac{\left(\alpha_{2}-\lambda_{2}\right) \alpha_{2}}{\theta}$. There exists a value $\theta_{3}$ such that if $\theta>\theta_{3}$, then $B\left(\alpha_{1}, \alpha_{2}, \lambda_{1}, \lambda_{2}, \theta, k\right)>0$. Let us consider the function $D\left(\alpha_{1}, \alpha_{2}\right.$, $\left.\lambda_{1}, \lambda_{2}, \theta, k\right)$. Also about $D$, there exists a value $\theta_{4}$ such that if $\theta>\theta_{4}$, then $D>0$. Define $\theta_{1}=\theta_{1}\left(\alpha_{1}, \alpha_{2}, \lambda_{2}, k\right)$ by $\theta_{1}=\max \left\{\theta_{3}, \theta_{4}\right\}$. The proof is completed.

Thus we the following
Theorem 1. Fix the parameters $\alpha_{1}, \alpha_{2}, \lambda_{2}$ and $k$ such that $\alpha_{1}>\alpha_{2}, \alpha_{2}>\lambda_{2}$. Fix the parameter $\theta$ such that $\theta>\theta_{1}=\theta_{1}\left(\alpha_{1}, \alpha_{2}, \lambda_{2}, k\right)$. If there exists a value $\lambda_{1}^{0}$ such that $F\left(\alpha_{1}, \alpha_{2}, \lambda_{1}^{0}, \lambda_{2}, \theta, k\right)>0$, then there exists a value $\lambda_{1}^{1}$ such that $\lambda_{1}^{0}<\lambda_{1}^{1}<\alpha_{2}-$ $\lambda_{2}, F\left(\alpha_{1}, \alpha_{2}, \lambda_{1}^{1}, \lambda_{2}, \theta, k\right)=0$ and as $\lambda_{1}$ is increased through $\lambda_{1}^{1}, F\left(\alpha_{1}, \alpha_{2}, \lambda_{1}, \lambda_{2}, \theta, k\right)$ changes its signature from positive to negative; i.e. a $\lambda_{1}-($ right $)$-branching appears at $\lambda_{1}^{1}$.

Proof. Lemma 2 shows that $\lambda_{1}$ can be increased to $\alpha_{2}-\lambda_{2}$, satisfying assumption (A). From the boundedness of $v_{f}$, we obtain

$$
\lim _{\lambda_{1} \rightarrow \alpha_{2}-\lambda_{2}} F=-\frac{\lambda_{2}}{k}<0
$$

This shows the existence of a value $\lambda_{1}^{1}$.
Similarly to Lemma 2 and Theorem 1, we can prove the following
Lemma 3. Fix the parameters $\alpha_{1}, \alpha_{2}, \lambda_{1}$ and $k$ such that $\alpha_{1}>\alpha_{2}, \alpha_{2}>\lambda_{1}$. There exists a value $\theta_{2}=\theta_{2}\left(\alpha_{1}, \alpha_{2}, \lambda_{1}, k\right)$ such that if $\theta>\dot{\theta}_{2}$, then condition $(A)$ is satisfied for every $\lambda_{2}$ such that $0<\lambda_{2}<\alpha_{2}-\lambda_{1}$.

Theorem 2. Fix the parameters $\alpha_{1}, \alpha_{2}, \lambda_{1}$ and $k$ such that $\alpha_{1}>\alpha_{2}, \alpha_{2}>\lambda_{1}$. Fix the parameter $\theta$ such that $\theta>\theta_{2}=\theta_{2}\left(\alpha_{1}, \alpha_{2}, \lambda_{1}, k\right)$. If there exists a value $\lambda_{2}^{0}$ such that $F\left(\alpha_{1}, \alpha_{2}, \lambda_{1}, \lambda_{2}^{0}, \theta, k\right)>0$, then there exists a value $\lambda_{2}^{1}$ such that $\lambda_{2}^{0}<\lambda_{2}^{1}<\alpha_{2}-$ $\lambda_{1}, F\left(\alpha_{1}, \alpha_{2}, \lambda_{1}, \lambda_{2}, \theta, k\right)=0$ and as $\lambda_{2}$ is increased through $\lambda_{2}^{1}, F\left(\alpha_{1}, \alpha_{2}, \lambda_{1}, \lambda_{2}\right.$, $\theta, k)$ changes its signature from positive to negative; i.e. a $\lambda_{2}$-(right)-branching appears at $\lambda_{2}^{1}$.

Define the function $G=G\left(\alpha_{1}, \alpha_{2}, \lambda_{2}, \theta, k\right)$ by $k \theta\left(\alpha_{2}-\lambda_{2}\right)\left(\alpha_{2}-\alpha_{1}\right)+\alpha_{2}^{2}$. The consideration of $F$ in the neighborhood of $\lambda_{1}=0$ gives the following

Theorem 3. Fix the parameters $\alpha_{1}, \alpha_{2}, \lambda_{2}, k$ such that $\alpha_{2}>\lambda_{2}, \alpha_{1}>\lambda_{2}$. If there exists a value $\lambda_{1}^{0}$ and $\theta$ such that $\theta>\theta_{0}=\theta_{0}\left(\alpha_{1}, \alpha_{2}, \lambda_{1}^{0}, \lambda_{2}, k\right), F\left(\alpha_{1}, \alpha_{2}, \lambda_{1}^{0}\right.$, $\left.\lambda_{2}, \theta, k\right)<0$ and $G\left(\alpha_{1}, \alpha_{2}, \lambda_{2}, \theta, k\right)>0$, then there exists a value $\lambda_{1}^{1}$ such that $0<\lambda_{1}^{1}<$ $\lambda_{1}^{0}, F\left(\alpha_{1}, \alpha_{2}, \lambda_{1}, \lambda_{2}, \theta, k\right)=0$ and as $\lambda_{1}$ is decreased through $\lambda_{1}^{1}, F\left(\alpha_{1}, \alpha_{2}, \lambda_{1}, \lambda_{2}, \theta, k\right)$ changes its signature from negative to positive; i.e. a $\lambda_{1}-(r i g h t)$-branching vanishes at $\lambda_{1}^{1}$.

Proof. From that $B\left(\alpha_{1}, \alpha_{2}, \lambda_{1}, \lambda_{2}, \theta, k\right)$ and $D\left(\alpha_{1}, \alpha_{2}, \lambda_{1}, \lambda_{2}, \theta, k\right)$ are monotone decreasing functions of $\lambda_{1}$, it follows that $\lambda_{1}$ can be decreased satisfying assumption (A). Notice that the function $F$ is considered as a function of $\lambda_{1}$ only and that $\frac{d F}{d \lambda_{1}}\left(\alpha_{1}, \alpha_{2}\right.$, $\left.0, \lambda_{2}, \theta, k\right)=\frac{\lambda_{2}}{k^{2} \theta \alpha_{1}\left(\alpha_{2}-\lambda_{2}\right)^{2}} G\left(\alpha_{1}, \alpha_{2}, \lambda_{2}, \theta, k\right)$. The condition that $G>0$ completes the proof.

Define the function $H=H\left(\alpha_{1}, \alpha_{2}, \theta, k\right)$ by $2 k \theta\left(\alpha_{2}-\alpha_{1}\right)+\alpha_{2}$. Similarly to Theorem 3 , we can prove the following

Theorem 4. Fix the parameters $\alpha_{1}, \alpha_{2}, \lambda_{2}$, and $k$ such that $\alpha_{2}>\lambda_{2}, \alpha_{1}>\lambda_{2}$. If there exists a value $\lambda_{2}^{0}$ and $\theta$ such that $\theta>\theta_{0}=\theta_{0}\left(\alpha_{1}, \alpha_{2}, \lambda_{1}, \lambda_{2}^{0}, k\right), F\left(\alpha_{1}, \alpha_{2}, \lambda_{1}\right.$, $\left.\lambda_{2}^{0}, \theta, k\right)<0$ and $H\left(\alpha_{1}, \alpha_{2}, \theta, k\right)>0$, then there exists a value $\lambda_{2}^{1}$ such that $0<\lambda_{2}^{1}<\lambda_{2}^{0}$, $F\left(\alpha_{1}, \alpha_{2}, \lambda_{1}, \lambda_{2}, \theta, k\right)=0$ and as $\lambda_{2}$ is decreased through $\lambda_{2}^{1}, F\left(\alpha_{1}, \alpha_{2}, \lambda_{1}, \alpha_{2}, \theta, k\right)$ changes its signature from negative to positive; i.e. a $\lambda_{2}$-(right)-branching vanishes at $\lambda_{2}^{1}$.

Remark. We give an example of parameters which satisfy the assumption of Theorem 3; $\alpha_{1}=0.7, \alpha_{2}=0.699, \lambda_{1}=0.3, \lambda_{2}=0.3, \theta=1000, k=1$. For this example, we get $F=-0.005315$ and $G=0.089601$.

## References

[1] G. H. Pimbley, Jr., Periodic solutions of predator-prey equations simulating an immune response I., Math. Biosci. 20 (1974), 27-51.
[2] G. H. Pimbley, Jr., Periodic solutions of third order predator-prey equations simulating an immune response., Arch. Rational Mech. Anal. 55 (1974), 93-123.

