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Global stability in some ecological models of commensalism between two species

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Abstract. Lyapunov functions for some mathematical models of ecological commensalism between two species are introduced. Global stability of the unique positive equilibrium is thereby established.

Keyword: *Models of ecological commensalism; Lyapunov's asymptotic stability theorem; Global stability*

1. Introduction

The species in an ecosystem will interact in different ways. These are mutualism and commensalism (regarded as positive interactions), and competition, amensalism, parasitism and predation (regarded as negative interactions).

In this paper we are interested in the commensal interactions. Commensal and mutualistic interactions occur frequently between species of terrestrial vertebrates (Dickman, 1992). Commensalism is a symbiotic relationship in which one partner benefits and the other partner appears neither to lose nor to gain from the relationship. Literature on the commensal interactions often

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argue for it in two way. The first is simply to assume that there is very little cost to the host (Goto et al., 2007; Lee et al., 2009). The second way argues that if large numbers of symbionts are tolerated by the host, then that means that they are harmless (Browne and Kingsford, 2005; Dvoretsky and Dvoretsky, 2009).

Mathematical modelling of interacting populations can provide valuable insights into variations of populations over time. Literature on the mathematical modelling of the negative interactions between species is very abundant, but modelling of positive interspecific interactions, particularly mutualistic ones, has generated interest in recent years (Graves et al., 2006; Legoviόc and Geek, 2012; Sun and Wei, 2003; Zhang, 2012).

Historically the first models that describes facultative mutualism are the following systems of ordinary differential equations (Addicott, 1981; Murray, 2002),

$$\frac{dn_1}{dt} = r_1 n_1 \left[1 - \frac{n_1}{K_1} + b_{12}\frac{n_2}{K_1}\right], \quad \frac{dn_2}{dt} = r_2 n_2 \left[1 - \frac{n_2}{K_2} + b_{21}\frac{n_1}{K_2}\right], \tag{1.1}$$

$$\frac{dn_1}{dt} = r_1 n_1 \left[1 - \frac{n_1}{K_1 + b_{12} n_2}\right], \frac{dn_2}{dt} = r_2 n_2 \left[1 - \frac{n_2}{K_2 + b_{21} n_1}\right], \tag{1.2}$$

where n_1 and n_2 are the density of species 1 and 2 at time t, respectively. The parameters r_i, K_i, $(i = 1, 2)$ b_{12} and b_{21} are all positive constants and, the r_i are the linear birth rates and the K_i are the carrying capacities. The b_{12} and b_{21} measure the cooperative effect of n_2 on n_1 and n_1 on n_2 respectively.

Now we propose ecological models to describe commensalism derivatives of the mutualist models. Recalling that commensalism (0,+) is the relation in which one of the species benefits, while another is not affected. The following conditions are satisfied: $b_{12} = 0$ and $b_{21} > 0$, the model of mutualism (1.2) becomes a model of commensalism:

$$\frac{dn_1}{dt} = r_1 n_1 \left[1 - \frac{n_1}{K_1}\right], \quad \frac{dn_2}{dt} = r_2 n_2 \left[1 - \frac{n_2}{K_2 + b_{21} n_1}\right]. \tag{1.3}$$

Similarly, if $b_{12} = 0$ and $b_{21} > 0$ the Lotka-Volterra system (1.1) becomes a Lotka-Volterra commensalism model

$$\frac{dn_1}{dt} = r_1 n_1 \left[1 - \frac{n_1}{K_1}\right], \quad \frac{dn_2}{dt} = r_2 n_2 \left[1 - \frac{n_2}{K_2} + b_{21}\frac{n_1}{K_2}\right]. \tag{1.4}$$

From the point of view of applications, a most interesting topic in population dynamics is the study of the global stability of equilibria. An important technique in stability theory for nonlinear differential equations is known as the second method of Lyapunov. A function with particular properties known as a Lyapunov function is constructed to prove global stability of equilibria in a given region. The construction of Lyapunov functions is often difficult for particular systems, but for Lotka-Volterra models, there has been some success.

The Volterra-type Lyapunov function $n - n^* - n^* \ln(n/n^*)$, has a long history of application to Lotka-Volterra systems and was originally discovered by Vito Volterra himself. In Lotka-Volterra models of two-species mutualism (1.1), Goh (1979) found sufficient conditions for global stability of unique positive equilibrium.

Recently, Vargas-De-León (2012) prove necessary and sufficient conditions for global stability of unique positive equilibrium to the mutualistic systems (1.1) and (1.2) subject to proportional harvesting, by means of elegant Lyapunov functions.

In this paper, we shall construct novel Lyapunov functions to study the global stability of the positive equilibrium of models of (1.3) and (1.4).

2. Global stability of positive equilibrium

It is easy to see that the non-negative quadrant

$$\mathcal{R}^2_+ = \left\{(n_1, n_2) \in \mathcal{R}^2 : n_1 \geq 0, n_2 \geq 0\right\}$$

is positively invariant with respect to (1.3) and (1.4), respectively.

Both systems (1.3) and (1.4) have the unique positive equilibrium (n_1^*, n_2^*) in $int(\mathcal{R}^2_+)$ with coordinates given by

$$n_1^* = K_1, \qquad n_2^* = K_2 + b_{21}K_1. \tag{2.5}$$

It follows from equations (2.5) that

$$\frac{K_2}{n_2^*} + b_{21}\frac{n_1^*}{n_2^*} = 1. \tag{2.6}$$

We establish that all solutions of (1.3) and (1.4) in $int(\mathcal{R}_+^2)$ converge to (n_1^*, n_2^*).

Theorem 2.1 *The unique positive equilibrium (n_1^*, n_2^*) of system (1.3) or (1.4) is globally asymptotically stable in the positive quadrant.*

Proof 1 *For the system (1.3) we define $L_1 : \left\{(n_1, n_2) \in \mathcal{R}_+^2 : n_1 > 0, n_2 > 0\right\} \to \mathcal{R}$ by*

$$L_1(n_1, n_2) = c_1 \int_{n_1^*}^{n_1} \frac{(\theta - n_1^*)}{(K_2 + b_{21}\theta)\theta^2} d\theta + c_2 \left(\ln \frac{n_2}{n_2^*} + \frac{n_2^*}{n_2} - 1 \right), \tag{2.7}$$

where $c_1 = r_2 c_2 (c_3 + b_{21} n_1^*)/r_1$, $c_2 > 0$ and $c_3 > 0$. The function $L_1(n_1, n_2)$ is defined, continuous and positive definite for all $n_1, n_2 > 0$. Also, the global minimum $L_1(n_1, n_2) = 0$ occurs at the positive equilibrium (n_1^*, n_2^*). Further, the time derivative of the function (2.7) along the trajectories of system (1.3), satisfies

$$\begin{aligned}
\frac{dL_1}{dt} &= \frac{r_2 c_2 (c_3 + b_{21} n_1^*)}{r_1 (K_2 + b_{21} n_1) n_1} \left(1 - \frac{n_1^*}{n_1}\right) \frac{dn_1}{dt} + \frac{c_2}{n_2}\left(1 - \frac{n_2^*}{n_2}\right)\frac{dn_2}{dt}, \\
&= \frac{r_2 c_2 (c_3 + b_{21} n_1^*)}{r_1 (K_2 + b_{21} n_1) n_1} \left(1 - \frac{n_1^*}{n_1}\right) \left[r_1 n_1 \left[1 - \frac{n_1}{K_1}\right]\right] \\
&+ \frac{c_2}{n_2}\left(1 - \frac{n_2^*}{n_2}\right) \left[r_2 n_2 \left[1 - \frac{n_2}{K_2 + b_{21} n_1}\right]\right], \\
&= \frac{r_2 c_2 (c_3 + b_{21} n_1^*)}{K_2 + b_{21} n_1} \left(1 - \frac{n_1^*}{n_1}\right) \left[1 - \frac{n_1}{K_1}\right] \\
&+ \frac{c_2 r_2}{K_2 + b_{21} n_1} \left(1 - \frac{n_2^*}{n_2}\right) \left[K_2 + b_{21} n_1 - n_2\right].
\end{aligned}$$

Using (2.6), we get

$$
\begin{aligned}
\frac{dL_1}{dt} &= \frac{r_2c_2(c_3+b_{21}n_1^*)}{K_2+b_{21}n_1}\left(1-\frac{n_1^*}{n_1}\right)\left(1-\frac{n_1}{n_1^*}\right) \\
&+ \frac{c_2r_2}{K_2+b_{21}n_1}\left(1-\frac{n_2^*}{n_2}\right)\left[K_2\left(1-\frac{n_2}{n_2^*}\right)+b_{21}n_1^*\left(\frac{n_1}{n_1^*}-\frac{n_2}{n_2^*}\right)\right], \\
&= \frac{r_2c_2(c_3+b_{21}n_1^*)}{K_2+b_{21}n_1}\left(2-\frac{n_1^*}{n_1}-\frac{n_1}{n_1^*}\right) \\
&+ \frac{c_2r_2}{K_2+b_{21}n_1}\left[K_2\left(1-\frac{n_2^*}{n_2}\right)\left(1-\frac{n_2}{n_2^*}\right)+b_{21}n_1^*\left(1-\frac{n_2^*}{n_2}\right)\left(\frac{n_1}{n_1^*}-\frac{n_2}{n_2^*}\right)\right], \\
&= \frac{r_2c_2c_3}{K_2+b_{21}n_1}\left(2-\frac{n_1^*}{n_1}-\frac{n_1}{n_1^*}\right)+\frac{r_2c_2}{K_2+b_{21}n_1}b_{21}n_1^*\left(2-\frac{n_1^*}{n_1}-\frac{n_1}{n_1^*}\right) \\
&+ \frac{c_2r_2}{K_2+b_{21}n_1}\left[K_2\left(2-\frac{n_2^*}{n_2}-\frac{n_2}{n_2^*}\right)+b_{21}n_1^*\left(\frac{n_1}{n_1^*}-\frac{n_2}{n_2^*}-\frac{n_1n_2^*}{n_1^*n_2}+1\right)\right],
\end{aligned}
$$

$$
\begin{aligned}
\frac{dL_1}{dt} &= \frac{r_2c_2c_3}{K_2+b_{21}n_1}\left(2-\frac{n_1^*}{n_1}-\frac{n_1}{n_1^*}\right)+\frac{c_2r_2K_2}{K_2+b_{21}n_1}\left(2-\frac{n_2^*}{n_2}-\frac{n_2}{n_2^*}\right) \\
&+ \frac{r_2b_{21}n_1^*c_2}{K_2+b_{21}n_1}\left[3-\frac{n_1^*}{n_1}-\frac{n_2}{n_2^*}-\frac{n_1n_2^*}{n_1^*n_2}\right], \\
&\le -\frac{r_2c_2c_3}{K_2+b_{21}n_1}\frac{n_1}{n_1^*}\left(1-\frac{n_1^*}{n_1}\right)^2-\frac{c_2r_2K_2}{K_2+b_{21}n_1}\frac{n_2}{n_2^*}\left(1-\frac{n_2^*}{n_2}\right)^2.
\end{aligned}
$$

For the system (1.4), we define $L_2:\left\{(n_1,n_2)\in\mathcal{R}_+^2 : n_1,n_2>0\right\}\to\mathcal{R}$ *by*

$$
L_2(n_1,n_2) = c_1\left(\ln\frac{n_1}{n_1^*}+\frac{n_1^*}{n_1}-1\right)+c_2\left(\ln\frac{n_2}{n_2^*}+\frac{n_2^*}{n_2}-1\right), \qquad (2.8)
$$

where $c_1 = r_2c_2(c_3+b_{21}n_1^*)/r_1K_2$, $c_2>0$ *and* $c_3>0$. *It is clear that at* (n_1^*,n_2^*) *the function* $L_2(n_1,n_2)$ *reaches its global minimum in* $\mathcal{R}_+^2$, *and hence* $L_2(n_1,n_2)$ *is a Lyapunov function. The derivative of (2.8) with respect to* t *along solution curves of (1.4) is given by*

$$
\begin{aligned}
\frac{dL_2}{dt} &= \frac{r_2c_2(c_3+b_{21}n_1^*)}{r_1K_2}\frac{1}{n_1}\left(1-\frac{n_1^*}{n_1}\right)\frac{dn_1}{dt}+\frac{c_2}{n_2}\left(1-\frac{n_2^*}{n_2}\right)\frac{dn_2}{dt}, \\
&= \frac{r_2}{K_2}c_2(c_3+b_{21}n_1^*)\left(1-\frac{n_1^*}{n_1}\right)\left[1-\frac{n_1}{K_1}\right] \\
&+ \frac{c_2r_2}{K_2}\left(1-\frac{n_2^*}{n_2}\right)\left[K_2-n_2+b_{21}n_1\right].
\end{aligned}
$$

The derivative calculation of Lyapunov function are similar to the previous calculations. Using (2.6), we have

$$\begin{aligned}\frac{dL_2}{dt} &= \frac{r_2c_2c_3}{K_2}\left(2-\frac{n_1^*}{n_1}-\frac{n_1}{n_1^*}\right)+c_2r_2\left(2-\frac{n_2^*}{n_2}-\frac{n_2}{n_2^*}\right)\\ &+ \frac{r_2b_{21}n_1^*c_2}{K_2}\left[3-\frac{n_1^*}{n_1}-\frac{n_2}{n_2^*}-\frac{n_1n_2^*}{n_1^*n_2}\right],\\ &\leq -\frac{r_2c_2c_3}{K_2}\frac{n_1}{n_1^*}\left(1-\frac{n_1^*}{n_1}\right)^2-c_2r_2\frac{n_2}{n_2^*}\left(1-\frac{n_2^*}{n_2}\right)^2.\end{aligned}$$

Clearly, $dL_i(n_1,n_2)/dt<0$ $(i=1,2)$ strictly for all n_1, $n_2>0$ except the positive equilibrium (n_1^*,n_2^*) where $dL_i/dt=0$. Furthermore, $L_i(n_1,n_2)\to\infty$ as $n_1\to 0$ or $n_1\to\infty$, and $L_i(n_1,n_2)\to\infty$ as $n_2\to 0$ or $n_2\to\infty$. Therefore, we may conclude that function (2.7) or (2.8) are Lyapunov functions for systems (1.3) and (1.4) respectively, and that by the Lyapunov asymptotic stability theorem (Lyapunov, 1992), the positive equilibrium (n_1^*,n_2^*) is globally asymptotically stable in the interior of $\mathcal{R}_+^2$, when it exists. This proves Theorem 2.1.

Remark 1 *Our Lyapunov constructions are applied to the following two chemostat-type commensal models*

$$\frac{dn_1}{dt}=s-dn_1(t),\ \frac{dn_2}{dt}=r_2n_2\left[1-\frac{n_2}{K_2}+b_{21}\frac{n_1}{K_2}\right], \tag{2.9}$$

$$\frac{dn_1}{dt}=s-dn_1(t),\quad \frac{dn_2}{dt}=r_2n_2\left[1-\frac{n_2}{K_2+b_{21}n_1}\right]. \tag{2.10}$$

The proof of the global stability of the positive equilibria of the models (2.9) and (2.10) are obtained by the Lyapunov functions (2.11) and (2.12), respectively.

$$V_1(n_1,n_2) = c_1n_1^*\left(\frac{n_1}{n_1^*}-1-\ln\frac{n_1}{n_1^*}\right)+c_2\left(\ln\frac{n_2}{n_2^*}+\frac{n_2^*}{n_2}-1\right), \tag{2.11}$$

where $c_1=r_2c_2(c_3+b_{21}n_1^*)/sK_2=r_2c_2(c_3+b_{21}n_1^*)/dK_2n_1^*$, $c_2>0$ and $c_3>0$.

$$V_2(n_1,n_2) = c_1\int_{n_1^*}^{n_1}\frac{(\theta-n_1^*)}{(K_2+b_{21}\theta)\theta}d\theta+c_2\left(\ln\frac{n_2}{n_2^*}+\frac{n_2^*}{n_2}-1\right), \tag{2.12}$$

where $c_1=r_2c_2(c_3+b_{21}n_1^*)/s=r_2c_2(c_3+b_{21}n_1^*)/dn_1^*$, $c_2>0$ and $c_3>0$.

Remark 2 *The choice of the constant c_1 is crucial in the construction of negative definiteness of the time derivative of the Lyapunov functions. On the Lyapunov functions (2.7), (2.8), (2.11) and (2.12) is assumed that $c_3 > 0$, also be defined as $c_3 = c_2 > 0$ or $c_3 = 0$.*

Remark 3 *The Lyapunov function*

$$\ln \frac{n}{n^*} + \frac{n^*}{n} - 1,$$

is introduced by Korobeinikov to Leslie-Gower type prey-predator systems (Korobeinikov, 2001; Korobeinikov and Lee, 2009) and recently by Vargas-De-León (2012) to Lotka-Volterra mutualism systems.

3. *

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