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LIMITING BEHAVIOR FOR COMPETING SPECIES*

S. B. HSU†

Abstract. Two competition models concerning n species consuming a single, limited resource are discussed. One is based on the Holling-type functional response and the other on the Lotka–Volterra-type. The focus of the paper is on the asymptotic behavior of solutions. LaSalle’s extension theorem of Lyapunov stability theory is the main tool.

1. Introduction. This article is concerned with the limiting behavior, as $t \rightarrow +\infty$, for the solutions of the systems

$$(A) \quad \begin{aligned} S'(t) &= (S^{(0)} - S(t))D - \sum_{i=1}^n \frac{k_i x_i(t) S(t)}{a_i + S(t)}, \\ x_i'(t) &= \frac{m_i x_i(t) S(t)}{a_i + S(t)} - D_i x_i(t), \quad i = 1, \dots, n, \end{aligned}$$

where $S^{(0)}$, D , k_i , a_i , m_i , D_i are positive, and

$$(B) \quad \begin{aligned} S'(t) &= \gamma S(t) \left(1 - \frac{S(t)}{K}\right) - \sum_{i=1}^n k_i x_i(t) S(t), \\ x_i'(t) &= \alpha_i x_i(t) (S(t) - \beta_i), \quad i = 1, \dots, n, \end{aligned}$$

where γ , K , k_i , α_i , β_i are positive. Only the positive solutions are analyzed, because they are of realistic interest.

The system (A) describes n species, with populations x_i , $i = 1, \dots, n$, and death rates D_i , competing for a single, limited resource S . This generalizes the model in [2] by allowing species-specific death rates. The species are assumed to feed on the resource with a saturating functional response to the resource density. Specifically, we assume that Michaelis–Menten kinetics or the Holling “disc” model describe how feeding rates and birth rates change with increasing resource density. Close parallels of this model in nature are e.g. the planktonic communities of unicellular algae in lakes and oceans. The species receive nutrient input from streams draining eroding water sheds or continental margins, and in lakes from nutrient regeneration during spring and fall overturn. For a more detailed biological background, we refer to [2].

The system (B) which is a generalization of the model given by MacArthur [5], has been discussed by Leung [4]. This competition model is based on Lotka–Volterra dynamics. It is also applicable to the economic study of n groups exploiting a single life resource.

The mathematical feature of this paper is to apply LaSalle’s extension theorem of Lyapunov stability theory ([1] or [3]). This technique allows us to generalize the results in [2] and to give simple, elegant proofs.

2. LaSalle’s extensions theorem. We note the following definition and the theorem of LaSalle [3] which will be used in §§ 3 and 4. Let $(I): x' = f(x)$ be a system of differential equations. The vector-valued function $f(x)$ is continuous in x for $x \in \bar{G}$ where G is an open set in R^n . Let V be a C^1 function on R^n to R .

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DEFINITION. We say V is a *Lyapunov function* in G for (I) if $\dot{V} = \text{grad } V \cdot f \leq 0$ on G .

Let $E = \{x \in \bar{G} : \dot{V}(x) = 0\}$.

THEOREM. If V is a *Lyapunov function* in G for (I), then each bounded solution $x(t) \in G$ of (I), approaches M where M is the largest invariant set in E .

3. Model of Holling's-type. In this section, we will discuss the limiting behavior of solutions for the system (A). First we note the following lemmas, omitting the proofs (see [2]).

LEMMA 3.1. The solutions $S(t), x_i(t), i = 1, \dots, n$ of (A) are positive and bounded.

LEMMA 3.2. Let $b_i = m_i/D_i, \lambda_i = a_i/(b_i - 1), i = 1, \dots, n$. If

$$(i) \quad b_i \leq 1$$

or

$$(ii) \quad \lambda_i > S^{(0)},$$

then $\lim_{t \rightarrow \infty} x_i(t) = 0$.

Our basic hypothesis is

$$(H_n) \quad 0 < \lambda_1 \leq \lambda_2 \leq \dots \leq \lambda_n, \quad \lambda_1 < S^{(0)}.$$

The equations in (A) may be relabeled without loss of generality, so that the parameters λ_i are nondecreasing in i . We note that (H_n) is more general than the hypothesis in [2] which excludes equality of this parameter for the first species.

THEOREM 3.3. Let (H_n) hold.

(i) If $0 < \lambda_1 < \lambda_2 \leq \dots \leq \lambda_n$, then the solutions of (A) satisfy

$$(3.1) \quad \begin{aligned} \lim_{t \rightarrow \infty} S(t) &= \lambda_1, \\ \lim_{t \rightarrow \infty} x_1(t) &= x_1^* = \frac{(S^{(0)} - \lambda_1)(a_1 + \lambda_1)D}{k_1 \lambda_1}, \\ \lim_{t \rightarrow \infty} x_i(t) &= 0, \quad i = 2, 3, \dots, n. \end{aligned}$$

(ii) If $0 < \lambda_1 = \dots = \lambda_j < \lambda_{j+1} \leq \dots \leq \lambda_n$, for some $j, 2 \leq j \leq n$, then the trajectory of (A) approaches M , where

$$M = \left\{ (\lambda_1, x_1, \dots, x_j, 0, \dots, 0) : (S^{(0)} - \lambda_1)D = \sum_{i=1}^j \frac{k_i \lambda_i}{\lambda_i + a_i} x_i, x_i \geq 0, \quad i = 1, \dots, j \right\}.$$

Proof. A rearrangement of (A) yields

$$\begin{aligned} S'(t) &= (S^{(0)} - S(t))D - \sum_{i=1}^n \frac{k_i x_i(t) S(t)}{a_i + S(t)}, \\ x_i'(t) &= (m_i - D_i) \frac{S(t) - \lambda_i}{a_i + S(t)} x_i(t). \end{aligned}$$

Let

$$V(S, x_1, \dots, x_n) = S - \lambda_1 - \lambda_1 \cdot \ln \left(\frac{S}{\lambda_1} \right) + c_1 \left[(x_1 - x_1^*) - x_1^* \cdot \ln \left(\frac{x_1}{x_1^*} \right) \right] + \sum_{i=2}^n c_i x_i,$$

and $G = \{(S, x_1, \dots, x_n) : S > 0, x_i > 0, i = 1, \dots, n\}$. Choose $c_i = k_i/(m_i - D_i), i = 1, \dots, n$. Then the time derivative of V computed along solutions of the differential equation is

$$\dot{V} = (S - \lambda_1) \left[\frac{(S^{(0)} - S)}{S} D - \frac{k_1 x_1^*}{a_1 + S} \right] + \sum_{i=2}^n k_i (\lambda_1 - \lambda_i) \frac{x_i}{a_i + S}$$

or

$$(3.2) \quad \dot{V} = \frac{(S - \lambda_1)^2 D}{(a_1 + S) S \lambda_1} (-\lambda_1 S - a_1 S^{(0)}) + \sum_{i=2}^n k_i (\lambda_1 - \lambda_i) \frac{x_i}{a_i + S} \leq 0 \quad \text{on } G.$$

If $0 < \lambda_1 < \lambda_2 \leq \dots \leq \lambda_n$, then

$$E = \{(\lambda_1, x_1, 0, \dots, 0) : x_1 \geq 0\}$$

and the largest invariant set M in E is $\{(\lambda_1, x_1^*, 0, \dots, 0)\}$. Hence (3.1) follows directly from Lemma 3.1 and LaSalle's theorem.

If $0 < \lambda_1 = \dots = \lambda_j < \lambda_{j+1} \leq \dots \leq \lambda_n$ for some $j, 2 \leq j \leq n$, then from (3.2) we have

$$E = \{(\lambda_1, x_1, \dots, x_j, 0, \dots, 0) : x_1, \dots, x_j \geq 0\}$$

and

$$M = \left\{ (\lambda_1, x_1, \dots, x_j, 0, \dots, 0) : (S^{(0)} - \lambda_1) D = \sum_{i=1}^j \frac{k_i \lambda_1}{a_i + \lambda_1} x_i, x_i \geq 0, i = 1, \dots, j \right\}.$$

Hence the trajectory approaches M .

4. Remark on the model of Lotka-Volterra. The arguments of § 3 can be modified to give a short proof for the behavior of solutions of system (B), considered in [4].

We note the following lemmas which are easy to prove:

1) The solutions of the system (B) are positive and bounded. 2) If $K < \beta_i$, for any $i = 1, \dots, n$, then $\lim_{t \rightarrow \infty} x_i(t) = 0$.

The basic hypothesis is

$$(H'_n) \quad 0 < \beta_1 \leq \beta_2 \leq \dots \leq \beta_n, \quad \beta_1 < K.$$

Using these lemmas and the Lyapunov function

$$V(S, x_1, \dots, x_n) = S - \beta_1 - \beta_1 \cdot \ln \left(\frac{S}{\beta_1} \right) + \frac{k_1}{\alpha_1} \left[(x_1 - x_1^*) - x_1^* \cdot \ln \left(\frac{x_1}{x_1^*} \right) \right] + \sum_{i=2}^n \frac{k_i}{\alpha_i} x_i,$$

where $x_i^* = (\gamma/k_i)(1 - (\beta_i/K))$, one can show that $\dot{V} = -(\gamma/K)(S - \beta_1)^2 + \sum_{i=2}^n (\beta_1 - \beta_i) k_i x_i \leq 0$ on $G = \{(S, x_1, \dots, x_n) : S > 0, x_i > 0, i = 1, \dots, n\}$.

If $0 < \beta_1 < \beta_2 \leq \dots \leq \beta_n$, then $E = \{(\beta_1, x_1, 0, \dots, 0) : x_1 \geq 0\}$ and $M = \{(\beta_1, x_1^*, 0, \dots, 0)\}$.

If $0 < \beta_1 = \beta_2 = \dots = \beta_j < \beta_{j+1} \leq \dots \leq \beta_n$ for some $j, 2 \leq j \leq n$, then $E = \{(\beta_1, x_1, \dots, x_j, 0, \dots, 0) : x_i \geq 0, i \leq j\}$ and $M = \{(\beta_1, x_1, \dots, x_j, 0, \dots, 0) \in E : \gamma(1 - (\beta_1/K)) = \sum_{i=1}^j k_i x_i\}$.

Let Ω be the w -limit set of the trajectory $(S(t), x_1(t), \dots, x_n(t))$ with the initial values $S(0) = S_0, x_i(0) = x_{i0}, 1 \leq i \leq n$. Let k be an integer such that $\alpha_k = \min_{1 \leq k \leq j} \{\alpha_i\}$. Since $\beta_1 = \dots = \beta_j$, from (B) it follows that

$$x_i(t) = x_{i0} x_{k0}^{-\alpha_i/\alpha_k} (x_k(t))^{\alpha_i/\alpha_k}, \quad 1 \leq i \leq j.$$

Hence

$$\begin{aligned}\Omega \subseteq & \left\{ (\beta_1, x_1, \dots, x_j, 0, \dots, 0) \in E : \gamma \left(1 - \frac{\beta_1}{K} \right) \right. \\ & \left. = \sum_{i=1}^j k_i x_{i0} x_{k0}^{-\alpha_i/\alpha_k} x_k^{\alpha_i/\alpha_k}, \quad x_i = x_{i0} x_{k0}^{-\alpha_i/\alpha_k} x_k^{\alpha_i/\alpha_k}, \quad 1 \leq i \leq j \right\}.\end{aligned}$$

From Theorem 1 in [4], there exists the unique positive root $x_k = \bar{x}_{k0}$ for the equation

$$\gamma \left(1 - \frac{\beta_1}{K} \right) = \sum_{i=1}^j k_i x_{i0} \bar{x}_{k0}^{-\alpha_i/\alpha_k} \bar{x}_{k0}^{\alpha_i/\alpha_k}.$$

By the assumption $\beta_1 < K$, we have

$$\Omega = \{(\beta_1, \bar{x}_{10}, \dots, \bar{x}_{j0}, 0, \dots, 0)\}, \quad \text{where } \bar{x}_{i0} = x_{i0} x_{k0}^{-\alpha_i/\alpha_k} \bar{x}_{k0}^{\alpha_i/\alpha_k}.$$

In either case, the results in [4] follow.

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