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COMPETING PREDATORS*

S. B. HSU[†], S. P. HUBBELL[‡] AND PAUL WALTMAN[¶]

Abstract. This paper concerns the growth of two predator species competing exploitatively for the same prey population. The prey are assumed to regenerate in the absence of predation by logistic growth. The predators are assumed to feed on the prey with a saturating functional response to prey density. Specifically, we assume that Michaelis–Menten kinetics or the Holling “disc” model describe how feeding rates and birth rates change with increasing prey density. We focus on the question as to when the competitive exclusion principle holds, given the growth parameters of the prey and the functional response parameters of the two predators. Which predator wins or loses depends critically on the relative magnitude of the prey carrying capacity, K , and the λ parameters of the two predators. (The parameter λ_i is the ratio of the i th predator’s Michaelis–Menten (half-saturation) constant to its intrinsic rate of increase, times its death rate.) Coexistence for the predators also appears possible for a wide range of parameters.

1. Introduction. In a previous paper [7], the authors analyzed an $(n + 1)$ -dimensional dynamical system which corresponds to the competition of n species for a single, essential nutrient in limited supply. The system modeled a chemostat, a laboratory apparatus used for the production and physiological study of microorganisms. In the chemostat model, the limiting nutrient is supplied at a constant rate. The input flow of medium contains all other factors for growth in excess. The output flow equals the input flow, and carries with it cells, waste products, and unused nutrients. The system also approximates conditions for plankton growth in lakes, with the input of limiting nutrients such as silica and phosphate from streams draining the surrounding watershed.

An important advance of this model over classical Lotka–Volterra formulations of competition is that the limiting resource for which competition is being expressed is represented explicitly by an equation in the system. In the Lotka–Volterra model, only the numbers of competing organisms are represented. The result of leaving out an equation for the resource is that the outcome of competition cannot be predicted before the organisms are actually grown together. In the present formulation, the outcome of competition can be predicted before the organisms compete, from measurements of growth parameters of the organisms when grown alone on the resource. This advance brings the theory of competition one step closer to being truly predictive rather than merely descriptive *ex post facto*.

In this paper and a companion paper [8], we continue this approach. Instead of a constant input of limiting nutrient, however, we now consider a renewable resource with reproductive properties—a more classic prey. Otherwise, the dynamics remain as in [7]. In particular, all of the parameters relative to the outcome of competition are measurable by experiments involving a single predator grown on the prey population. The division between this paper and [8] is that here we present a precise statement of the theorems and their proofs, while [8] contains the biological background and a less precise but a more biologically meaningful statement of these results and the results of [7], along with a discussion of certain experiments whose results these theorems help to explain. The companion paper also presents some numerical examples and some

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speculations. The ideas developed in the proofs here may be of use to mathematicians working on other dynamical systems.

In the case of a renewable resource, the example of McGehee and Armstrong [11] and the numerical experiments of Koch [9] and the authors [8], lead one not to expect the competitive exclusion principle to hold throughout all of the parameter space. The theorems presented in § 3 attempt to determine regions of the parameter space where competitive exclusion does hold. The proofs of these theorems are given in § 4, and the model itself is described in § 2. The separation of the work into a formal, theoretical component and a biological component [8] comes as a result of referees' suggestions.

2. Statement of the model. The present analysis concerns the behavior of a predator-prey system consisting of two predator species, x_1 and x_2 , and a single prey species, S . We specifically assume that the predator species compete purely exploitatively, with no interference between rivals (no toxins are produced, for example). Both species have access to the prey and compete only by lowering the population of shared prey. For death rates it is assumed that the number dying is proportional to the number currently alive. We also assume that there are no significant time lags in the system, that growth rates are logistic in the prey species in the absence of predation, and that the predators' functional response obeys the Holling "nonlearning" curve [5], [6]. The model is given by:

$$\begin{aligned}
 S'(t) &= \gamma S(t) [1 - S(t)/K] - \left(\frac{m_1}{y_1} \right) \left(\frac{x_1(t)S(t)}{a_1 + S(t)} \right) - \left(\frac{m_2}{y_2} \right) \left(\frac{x_2(t)S(t)}{a_2 + S(t)} \right), \\
 x_1'(t) &= \frac{m_1 x_1(t) S(t)}{a_1 + S(t)} - D_1 x_1(t), \\
 x_2'(t) &= \frac{m_2 x_2(t) S(t)}{a_2 + S(t)} - D_2 x_2(t), \\
 S(0) &= S_0 > 0, \quad x_1(0) = x_{10} > 0, \quad x_2(0) = x_{20} > 0,
 \end{aligned}
 \tag{2.1}$$

where $x_i(t)$ is the number of the i th predator at time t , $S(t)$ is the number of the prey at time t , m_i is the maximum growth ("birth") rate of the i th predator, D_i is the death rate for the i th predator, y_i is the yield factor for the i th predator feeding on the prey, a_i is the half-saturation constant for the i th predator, which is the prey density at which the functional response of the predator is half maximal. The parameters γ and K are the intrinsic rate of increase and the carrying capacity for the prey population, respectively.

We analyze the behavior of solutions of this system of ordinary differential equations in order to answer the biological question: Under what conditions will neither, one, or both species of predator survive? If only one predator survives, we also seek to determine the limiting behavior of the surviving predator and its prey. As noted in the introduction, the biological background and references, the experiments which our results help clarify, etc., may be found in Hsu, Hubbell, and Waltman [8].

3. Statement of results. In this section we state the principal results of the paper. The proofs and certain technical lemmas are deferred to the next section. The first lemma is a statement that the system given by (2.1) is as "well-behaved" as one intuits from the biological problem.

LEMMA 3.1. *Solutions of (2.1) are bounded and remain in the positive octant.*

The next lemma provides conditions under which the predators cannot survive on

the prey, given the carrying capacity of the prey population, even in the absence of competition:

LEMMA 3.2. *A necessary condition for either species x_i to survive is $0 < \lambda_i < K$.*

This lemma states that if the maximum birth rate, m_i , is less than or equal to the death rate, D_i , or if the parameter λ_i is greater than or equal to the carrying capacity of the prey, then the i th predator will die out, independent of competition from the rival predators. This establishes that there is a minimum population size which can support a given predator: K must be larger than λ_i for the i th predator to survive, independent of competition.

We state the principal result in the case of inadequate carrying capacity ($\lambda_i > K$ for $i = 1$ or 2) or inadequate growth ($b_i \leq 1$, $i = 1$ or 2) in three parts. We are able in Theorem 3.3 to determine the asymptotic behavior of the solutions or to assert the existence of limiting periodic solutions. The theorem may be summarized as the unsuccessful competitor does not affect the eventual behavior of the survivors.

First we consider the case where either the carrying capacity or the maximum growth rate is inadequate for either predator species to survive. As one expects, in this case the prey grows to carrying capacity.

THEOREM 3.3(i): *If (a) $b_1 \leq 1$ or $\lambda_1 > K$, and
(b) $b_2 \leq 1$ or $\lambda_2 > K$,*

then $\lim_{t \rightarrow \infty} S(t) = K$ and $\lim_{t \rightarrow \infty} x_i(t) = 0$, $i = 1, 2$.

For the remainder of the theorem, we assume $0 < \lambda_1 < K$.

THEOREM 3.3 (ii): *Let (a) $0 < \lambda_1 < K$, and
(b) $\lambda_2 > K$ or $b_2 \leq 1$.*

If $K < a_1 + 2\lambda_1$, then

$$\lim_{t \rightarrow \infty} S(t) = S^* = \lambda_1,$$

$$\lim_{t \rightarrow \infty} x_1(t) = x_1^* = \frac{\gamma(1 - S^*/K)(a_1 + S^*)}{(m_1/y_1)}$$

$$\lim_{t \rightarrow \infty} x_2(t) = 0.$$

THEOREM 3.3 (iii): *Suppose that (a) $0 < \lambda_1 < K$, and
(b) $\lambda_2 > K$ or $b_2 \leq 1$.*

If $K > a_1 + 2\lambda_1$, then the omega limit set of the trajectory of $(S(t), x_1(t), x_2(t))$ lies in the $S - x_1$ plane (i.e., $\lim_{t \rightarrow \infty} x_2(t) = 0$) and contains a periodic trajectory except for one distinguished orbit which approaches the critical point $(S^, x_1^*, 0)$.*

Our principal result, when the carrying capacity of the prey is adequate for each predator species to survive, is contained in Theorem 3.4. This theorem adds a large region in the parameter space to that determined in Theorem 3.3 where coexistence is not possible.

THEOREM 3.4. *Suppose that $0 < \lambda_1 < \lambda_2 < K$ and $b_1 \geq b_2$. The conclusion of Theorem 3.3 (ii) holds if $K < a_1 + 2\lambda_1$ and the conclusion of Theorem 3.3 (iii) holds if $K > a_1 + 2\lambda_1$.*

A numerical example in [8] shows that coexistence is possible when the hypotheses of Theorem 3.4 are violated. Although the problem remains open analytically, we have the following partial result.

THEOREM 3.5. *Suppose that $0 < \lambda_1 < \lambda_2 < K$, $a_1 < a_2$ and $K < a_2 + 2\lambda_2$. Then $\limsup_{t \rightarrow \infty} x_1(t) > 0$.*

In the simulation in [8], the following result was useful particularly when $b_2 - b_1$ was small.

THEOREM 3.6. *Suppose that $0 < \lambda_1 < \lambda_2 < K$, $a_1 < a_2$, $b_1 < b_2$, and $K < (b_1 a_2 - b_2 a_1) / (b_2 - b_1)$. Then $\lim_{t \rightarrow \infty} x_2(t) = 0$.*

4. Proofs.

Proof of Lemma 3.1. Since $S_0 > 0$ and $x_{i0} > 0$, $i = 1, 2$, uniqueness of solutions of initial value problems keeps the trajectory in the positive octant. Since $S'(t) \leq \gamma S(t)(1 - S(t)/K)$, $S(t)$ may be compared with solutions of

$$z'(t) = \gamma z(t) \left(1 - \frac{z(t)}{K} \right), \quad z(0) = S_0$$

to yield

$$(4.1) \quad S(t) \leq \frac{K}{1 + C_0 e^{-\gamma t}} \quad \text{for } t \geq 0,$$

where $C_0 = K - S_0/S_0$. The boundedness of $x_i(t)$ follows readily using a bound on $S(t)$.

Proof of Lemma 3.2. If $b_i \leq 1$ then from the representation

$$x_i(t) = x_{i0} \exp \int_0^t \left(\frac{(m_i - D_i)S(\xi) - a_i D_i}{a_i + S(\xi)} \right) d\xi,$$

it follows that $\lim_{t \rightarrow \infty} x_i(t) = 0$, while if $\lambda_i > K$ then a slight rearrangement,

$$x_i(t) = x_{i0} \exp \int_0^t \left(\frac{m_i - D_i}{a_i + S(\xi)} \right) \left(S(\xi) - \frac{a_i}{b_i - 1} \right) d\xi,$$

and the use of a bound on $S(t)$ easily yields the same conclusion. Only $\lambda_i = K$ remains.

LEMMA 4.1 (Coppel [4, p. 141]). *If a function $f(t)$ has a finite limit as $t \rightarrow \infty$ and $f^n(t)$ (the n -th derivative) is bounded for $t \geq t_0$, then $\lim_{t \rightarrow \infty} f^k(t) = 0$, $0 < k < n$.*

In the half space $S \geq K$, $S'(t) < 0$ except at the critical point $(K, 0, 0)$ and hence no point of the plane $S = K$ can be in the omega limit set of a trajectory except for this critical point and further the function $x_i(t)$ can change sign at most once. Thus $\lim_{t \rightarrow \infty} x_i(t) = x_i^*$ exists. Suppose $x_i^* > 0$. Since the right-hand side of the equation is bounded, $\lim_{t \rightarrow \infty} x'(t) = 0$ or, by Lemma 4.1, $\lim_{t \rightarrow \infty} S(t) = K$. Thus a trajectory has an omega limit point of the form (K, x_1^*, x_2^*) with $x_i^* > 0$, a contradiction. Hence $x_i^* = 0$.

Before beginning the proof of Theorem 3.3(i), we note the following definitions and a theorem of Markus [10] which will be used here and in the proof of Theorem 3.5.

DEFINITION. Let $A: x'_i = f_i(x, t)$ and $A_\infty: x'_i = f_i(x)$ ($i = 1, 2, \dots, n$) be a first order system of ordinary differential equations. The real-valued functions $f_i(x, t)$ and $f_i(x)$ are continuous in (x, t) for $x \in G$, where G is an open subset of \mathbb{R}^n , and for $t > t_0$, and they satisfy a local Lipschitz condition in x . A is said to be asymptotic to A_∞ ($A \rightarrow A_\infty$) in G if for each compact set $K \subset G$ and for each $\varepsilon > 0$, there is a $T = T(K, \varepsilon) > t_0$ such that $|f_i(x, t) - f_i(x)| < \varepsilon$ for all $i = 1, 2, \dots, n$, all $x \in K$, and all $t > T$.

THEOREM (Markus). *Let $A \rightarrow A_\infty$ in G and let P be an asymptotically stable critical point of A_∞ . Then there is a neighborhood N of P and a time T such that the omega limit set for every solution $x(t)$ of A which intersects N at a time later than T is equal to P .*

Proof of Theorem 3.3(i). From Lemma 3.2, it follows that $\lim_{t \rightarrow \infty} x_i(t) = 0$, $i = 1, 2$. We will show that if these limits are zero then $\lim_{t \rightarrow \infty} S(t) = K$. The omega limit set, Ω , of a trajectory of (2.1), $(S(t), x_1(t), x_2(t))$ lies on the S -axis i.e. $\Omega \subseteq \{(S, 0, 0), S \geq 0\}$. It is not hard to show that Ω contains a point $(S_1, 0, 0)$, $S_1 > 0$, from which then it readily follows that $(K, 0, 0) \in \Omega$.

Applying the Markus theorem to

$$A : S' = \gamma S \left(1 - \frac{S}{K} \right) - \sum_{i=1}^2 \frac{m_i S x_i(t)}{y_i a_i + S}$$

$$S(0) = S_0,$$

and

$$A_\infty : S' = \gamma S \left(1 - \frac{S}{K} \right),$$

$$S(0) = S_0 > 0,$$

it follows that $\lim_{t \rightarrow \infty} S(t) = K$.

The next lemma provides a necessary condition for both species x_1 and x_2 to become extinct. A proof, by contradiction, is straightforward and is omitted.

LEMMA 4.2. *If $\lim_{t \rightarrow \infty} x_i(t) = 0$, $i = 1, 2$, then $(m_i - D_i)/(a_i m_i) \leq 1/(a_i + K)$, $i = 1, 2$.*

Before we explore the behavior of the solutions of (2.1), we need some facts about the behavior of the solutions of the two dimensional system,

$$S'(t) = \gamma S(t) \left(1 - \frac{S(t)}{K} \right) - \frac{m x(t) S(t)}{y a + S(t)},$$

$$(4.2) \quad x'(t) = \frac{m x(t) S(t)}{a + S(t)} - D_0 x(t),$$

$$S(0) = S_0 > 0, \quad x(0) = x_0 > 0;$$

where γ, K, m, y, D_0 are positive constants. As in Lemma 3.1, it follows that

(4.3) the solutions $S(t), x(t)$ of (4.2) are positive and bounded.

LEMMA 4.3. *Let $b^* = m/D_0$.*

(i) *If $b^* \leq 1$ or $K < a/(b^* - 1)$ then the critical point $(K, 0)$ of (4.2) is asymptotically stable.*

(ii) *If $b^* > 1$ and $a/(b^* - 1) < K < a + 2a/(b^* - 1)$ then the critical point (\hat{S}, \hat{x}) , $\hat{S} = a/(b^* - 1)$, $\hat{x} = (\gamma y/m)(1 - \hat{S}/K)(a + \hat{S})$, of (4.2) is asymptotically stable. If $b^* > 1$ and $K > a + 2a/(b^* - 1)$, then (\hat{S}, \hat{x}) is unstable.*

Proof. Standard arguments using the variational equation provide a direct proof.

LEMMA 4.4. *If $0 < a/(b^* - 1) < K \leq a + 2a/(b^* - 1)$ then (4.7) has no limit cycles in the first quadrant of the S - x plane.*

Proof. The absence of limit cycles will follow from a theorem of Dulac; see Andronov, Leontovich, Gordon and Maier [3, p. 205]. Let

$$f_1(S, x) = \gamma S \left(1 - \frac{S}{K} \right) - \frac{m S x}{y a + S}$$

$$f_2(S, x) = \frac{m S x}{a + S} - D_0 x$$

and

$$h(S, x) = \left(\frac{S}{a + S} \right)^\alpha x^\delta, \quad S > 0, \quad x > 0,$$

where $\alpha, \delta \in \mathbf{R}$ will be selected below. The Dulac theorem states that there will be no limit cycle if the expression $\partial(f_1h)/\partial S + \partial(f_2h)/\partial x$ does not change sign. This expression can be computed as

$$(4.4) \quad \frac{\partial f_1 h}{\partial S} + \frac{\partial f_2 h}{\partial x} = -\frac{m}{y} \cdot ax^{\delta+1} S^\alpha (a+S)^{-(\alpha+2)} (\alpha+1) + \gamma x^\delta S^\alpha (a+S)^{-(\alpha+1)} P_{\alpha,\beta}(S)$$

where $\beta = (\delta+1)/\gamma$, and

$$(4.5) \quad P_{\alpha,\beta}(S) = \left(-\frac{2}{K}\right) S^2 + \left(\beta(m-D_0) + \left(1 - \frac{(\alpha+2)a}{K}\right)\right) S + a[(\alpha+1) - \beta D_0].$$

We seek to choose α and β . By Lemma 3.1 and (4.3), (4.4), the lemma will be proved by selecting values of α, β such that $\alpha \geq -1$ and the expression $P_{\alpha,\beta}(S) \leq 0$ for $S > 0$. To do this we first look at the quadratic $p_{\alpha,\beta}(S)$. The discriminant $D_\alpha(\beta)$ of $P_{\alpha,\beta}(S)$ is given by

$$(4.6) \quad \begin{aligned} D_\alpha(\beta) = & \beta^2(m-D_0)^2 + 2\beta \left[(m-D_0) \left(\left(1 - \frac{a(\alpha+2)}{K}\right) - \frac{4aD_0}{K} \right) \right] \\ & + \left(1 - \frac{a(\alpha+2)}{K}\right)^2 + \frac{8a}{K}(\alpha+1), \end{aligned}$$

and in turn the discriminant $D(\alpha)$ of the quadratic form $D_\alpha(\beta)$ is given by

$$(4.7) \quad D(\alpha) = \frac{32a}{K^2} [\alpha \{ (m-D_0)(aD_0 - K(m-D_0)) \} + m(2aD_0 - K(m-D_0))].$$

If there is an α^* such that $D(\alpha^*) > 0$, then $D_{\alpha^*}(\beta) = 0$ has two real roots β_1, β_2 . If β^* is any real number such that $\beta_1 < \beta^* < \beta_2$ then $D_{\alpha^*}(\beta) < 0$ and $P_{\alpha^*,\beta^*}(S) = 0$ has no real roots. Since the coefficient of S^2 is negative $P_{\alpha^*,\beta^*}(S) < 0$ for all S . Choosing $\delta^* = \gamma\beta^* - 1$ completes the argument.

If $K < 2a/(b^* - 1)$, choose $\alpha^* = 0$. For $K = 2a/(b^* - 1)$, any $\alpha^* > 0$ will do. For $0 < 2a/(b^* - 1) < K < a + 2a/(b^* - 1)$, choose α^* such that

$$-1 < \alpha^* < \frac{m[2aD_0 - K(m-D_0)]}{(m-D_0)[K(m-D_0) - aD_0]} < 0$$

and it follows that $D(\alpha^*) > 0$.

If $K = a + 2a/(b^* - 1)$, choose $\alpha^* = -1$. It follows that $D_{\alpha^*}(\beta) = (m-D_0)^2(\beta - \beta^*)^2$ where β^* is the double root of $D_{\alpha^*}(\beta) = 0$. If one chooses $\beta = \beta^*$ then it follows that $P_{\alpha^*,\beta^*}(S) = -2/K(S - S_*)^2$ for some S_* or $P_{\alpha^*,\beta^*}(S) \leq 0$.

The following lemma gives a complete classification of the behavior of the solutions of (4.2).

LEMMA 4.5. Let $S(t), x(t)$ be the solutions of (4.2).

(i) If $b^* \leq 1$ or $0 < K \leq a/(b^* - 1)$, then

$$\lim_{t \rightarrow \infty} S(t) = K \text{ and } \lim_{t \rightarrow \infty} x(t) = 0.$$

(ii) If $0 < a/(b^* - 1) < K \leq a + 2a/(b^* - 1)$, then

$$\lim_{t \rightarrow \infty} S(t) = a/(b^* - 1) = \hat{S}$$

and $\lim_{t \rightarrow \infty} x(t) = (\gamma y/m)(1 - \hat{S}/K)(a + \hat{S}) = \hat{x}$.

(iii) If $K > a + 2a/(b^* - 1)$, then there exists at least one periodic orbit in the first quadrant of the S - x plane. If there is just one periodic orbit, it is stable. If the periodic

orbit is not unique, then the outer one is semistable from the outside and the inner one is semistable from the inside.

Proof. The proof of (i) follows from the arguments used in providing Lemma 3.2 and Theorem 3.1(i) and by using Lemma 4.1 the proof of (ii) follows from Lemma 4.4 while (iii) follows from the Poincaré–Bendixson theorem. We note that the uniqueness of the limit cycle has not been established; [1] and [2] show that this can be a delicate question.

We return now to system (2.1). An analysis of the variational equation provides the proof of the next lemma.

LEMMA 4.6. *Let $0 < \lambda_1 < K < a_1 + 2\lambda_1$. If $b_2 \leq 1$ or if $\lambda_1 < \lambda_2$ then the critical point $(S^*, x_1^*, 0)$ is asymptotically stable, where $S^* = \lambda_1$, $x_1^* = \gamma \left(1 - \frac{S^*}{K}\right) (a_1 + S^*) / (m_1 / y_1)$.*

For convenience we note the following two statements: $b_i \leq 1$ or $0 < K < \lambda_i$ is equivalent to

$$(4.8) \quad \frac{m_i - D_i}{a_i m_i} < \frac{1}{a_i + K}.$$

$$(4.9) \quad K > \lambda_i > 0 \text{ is equivalent to } \frac{m_i - D_i}{a_i m_i} > \frac{1}{a_i + K}.$$

Proof of Theorem 3.3(ii). From (4.8), (4.9), Lemma 3.2 and Lemma 4.2, it follows that $\lim_{t \rightarrow \infty} x_2(t) = 0$ and $\limsup_{t \rightarrow \infty} x_1(t) > 0$. If $\lim_{t \rightarrow \infty} x_i(t)$ exists and is equal to $c > 0$, then since by Lemma 3.1, $x_1''(t)$ is bounded, Lemma 4.1 implies that $\lim_{t \rightarrow \infty} S(t) = \lambda_1$. Again using Lemma 3.1, $S''(t)$ is bounded and hence $\lim_{t \rightarrow \infty} S'(t) = 0$ and

$$c = x_1^* = \frac{\gamma [1 - S^*/K] (a_1 + S^*)}{(m_1 / y_1)}.$$

If $\lim_{t \rightarrow \infty} x_1(t)$ does not exist, choose a sequence $\{t_n\}$ such that $\lim_{n \rightarrow \infty} t_n = \infty$, $x_i(t_n)$ is a relative maximum, $x_1(t_n) > \varepsilon$ for some $\varepsilon > 0$, for all n and $\lim_{n \rightarrow \infty} x_1(t_n) = x_{1\omega}$ for some $x_{1\omega} \geq \varepsilon > 0$. By (2.1), we have $S(t_n) = a_1 / (b_1 - 1) = \lambda_1 = S^*$. Then $(S^*, x_{1\omega}, 0) \in \Omega$ where Ω is the omega limit set of the solution $(S(t), x_1(t), x_2(t))$ of (2.1) and lies on S - X_1 plane. Using Lemma 4.5(ii) with $m = m_1$, $y = y_1$, $a = a_1$, $D_0 = D_1$, $b^* = b_1$, it follows that the solution of (2.1) with $S(0) = S^*$, $x_1(0) = x_{1\omega}$, $x_2(0) = 0$ satisfies $\lim_{t \rightarrow \infty} S(t) = S^*$, $\lim_{t \rightarrow \infty} x_1(t) = x_1^*$, $x_2(t) \equiv 0$. This and invariance property of the omega limit set imply that $(S^*, x_1^*, 0) \in \Omega$. However, $(S^*, x_1^*, 0)$ is asymptotically stable by Lemma 4.6. Hence the trajectory $(S(t), x_1(t), x_2(t))$ approaches the critical point $(S^*, x_1^*, 0)$. In particular, $\lim_{t \rightarrow \infty} x_1(t) = x_1^*$. This is the desired contradiction.

Proof of Theorem 3.3(iii). As above, from (4.8), (4.9), Lemma 3.2 and Lemma 4.2, it follows that $\lim_{t \rightarrow \infty} x_2(t) = 0$ and $\lim_{t \rightarrow \infty} \sup x_1(t) > 0$. The arguments used in Theorem 3.3(ii) yield that $(S^*, x_{1\omega}, 0) \in \Omega$ for some $x_{1\omega} > 0$. Let Ω' denote the omega limit set of the two dimension system $(x^2 \equiv 0)$ through $(S^*, x_{1\omega})$. The critical point $(\hat{S}; \hat{x})$ is unstable by Lemma 4.3 and the trajectory is bounded, so the Poincaré–Bendixson theorem implies that Ω' is a periodic solution. But $(\Omega', 0) \subset \Omega$ by the invariance property of omega limit sets. The existence of the distinguished orbit follows from Hartman’s linearization theorem.

The following lemma is similar to Lemma 4.3 of Hsu, Hubbell, and Waltman [7] and the proof is omitted.

LEMMA 4.7. *Let $0 < a_1 / (b_1 - 1) < a_2 / (b_2 - 1)$. If $b_2 \leq b_1$ then $\lim_{t \rightarrow \infty} x_2(t) = 0$.*

Proof of Theorem 3.4. (4.8), (4.9), Lemmas 4.2 and 4.7 imply that $\lim_{t \rightarrow \infty} x_2(t) = 0$ and $\limsup_{t \rightarrow \infty} x_1(t) > 0$. The same type of arguments used in the proof of Theorems 3.3(ii) and 3.3(iii) completes the proof of Theorem 3.4.

Proof of Theorem 3.5. If $\lim_{t \rightarrow \infty} x_1(t) = 0$, then by (4.9) and Lemma 4.2 it follows that $\limsup_{t \rightarrow \infty} x_2(t) > 0$. If $\lim_{t \rightarrow \infty} x_2(t) = c > 0$ then Lemma 4.1 implies that $\lim_{t \rightarrow \infty} S(t) = \lambda_2$ and hence $x_1(t)$ is unbounded, a contradiction. If $\lim_{t \rightarrow \infty} x_2(t)$ does not exist, then applying the same argument in Theorem 3.3(ii) yields $(\lambda_2, 0, x_{2\omega}) \in \Omega$ where Ω is the omega limit set of the solution $(S(t), x_1(t), x_2(t))$ of (2.1). Applying Lemma 4.5(ii) with $a = a_2, m = m_2, y = y_2, D_0 = D_2, b^* = b_2$ it follows that the solution of (2.1) with $S(0) = \lambda_2, x_1(0) = 0, x_2(0) = x_{2\omega}$ satisfies $\lim_{t \rightarrow \infty} S(t) = \lambda_2, x_1(t) \equiv 0, \lim_{t \rightarrow \infty} x_2(t) = x_2^* = \gamma \left(1 - \frac{\lambda_2}{K}\right) (a_2 + \lambda_2) / (m_2 / y_2) > 0$. This and the invariance property of the omega limit set imply $(\lambda_2, 0, x_2^*) \in \Omega$. Hence there exists $\{t_n\}$ such that $\lim_{n \rightarrow \infty} t_n = \infty, \lim_{n \rightarrow \infty} S(t) = \lambda_2$, and $\lim_{n \rightarrow \infty} x_2(t_n) = x_2^*$.

Now consider the following systems:

$$\begin{aligned}
 A: S' &= \gamma S \left(1 - \frac{S}{K}\right) - \frac{m_2}{y_2} \frac{x_2 S}{a_2 + S} - \frac{m_1}{y_1} \frac{x_1(t) S}{a_1 + S}, \\
 x_2' &= \frac{m_2 x_2 S}{a_2 + S} - D_2 x_2, \quad S(0) = S_0 > 0, \\
 x_2(0) &= x_{20} > 0, \\
 A_\infty: S' &= \gamma S \left(1 - \frac{S}{K}\right) - \frac{m_2}{y_2} \frac{x_2 S}{a_2 + S}, \\
 x_2' &= \frac{m_2 x_2 S}{a_2 + S} - D_2 x_2.
 \end{aligned}$$

Obviously $A \rightarrow A_\infty$ in $Q = \{(S, x_2) | S > 0, x_2 > 0\}$. Since (λ_2, x_2^*) is an asymptotically stable critical point of (A_∞) and since $\lim_{n \rightarrow \infty} S(t_n) = \lambda_2, \lim_{n \rightarrow \infty} x_2(t_n) = x_2^*$ for some $\{t_n\}$, then by Markus's theorem it follows that $\lim_{t \rightarrow \infty} S(t) = \lambda_2$ and $\lim_{t \rightarrow \infty} x_2(t) = x_2^* > 0$. Again this is a contradiction.

Proof of Theorem 3.6. Choose $\epsilon > 0$ such that $K + \epsilon < (b_1 a_2 - b_2 a_1) / (b_2 - b_1)$ and choose t_0 such that $S(t) \leq K + \epsilon$ for $t \geq t_0$. Then one has

$$\begin{aligned}
 \frac{x_2'(t)}{D_2 x_2(t)} - \frac{x_1'(t)}{D_1 x_1(t)} &= \frac{b_2 S(t)}{a_2 + S(t)} - \frac{b_1 S(t)}{a_1 + S(t)} \\
 &= S(t) \frac{(b_2 - b_1) S(t) - (b_1 a_2 + b_2 a_1)}{(a_1 + S(t))(a_2 + S(t))} \\
 &\leq S(t) \frac{(b_2 - b_1)(K + \epsilon) - (b_1 a_2 + b_2 a_1)}{(a_1 + K + \epsilon)(a_2 + K + \epsilon)}
 \end{aligned}$$

for $t \geq t_0$.

Since $\limsup_{t \rightarrow \infty} S(t) = \bar{S} > 0$ (a consequence of Lemma 4.1) and since $S'(t)$ is uniformly bounded, there are constants $\delta > 0$ and $\epsilon^* > 0$ and a sequence of disjoint intervals $I_n = (t_n - \delta, t_n + \delta), t_n \rightarrow \infty$, such that $S(t) > \epsilon^*$ for $t \in I_n$. In particular, $\lim_{t \rightarrow \infty} \int_{t_0}^t S(\eta) d\eta = +\infty$. Integrating the above inequality gives

$$\left(\frac{x_2(t)}{x_2(t_0)}\right)^{1/D_2} \leq \left(\frac{x_1(t)}{x_1(t_0)}\right)^{1/D_1} \exp\left(-C \int_{t_0}^t S(\eta) d\eta\right), \quad C > 0.$$

Hence it follows that $\lim_{t \rightarrow \infty} x_2(t) = 0$.

5. Discussion. This paper is an analysis of the behavior of a model of two predators competing exploitatively for a shared prey species. The prey grow logistically in the absence of predation, and the predators consume prey according to a saturating functional response. The analysis has dealt principally with three parameters: K , the carrying capacity of the prey, and parameters of the i th predator: a_i , the half saturation constant, and λ_i . The latter parameter is particularly important to the outcome of competition, and is the ratio of the i th predator's half saturation constant to its intrinsic rate of increase, times its death rate:

$$\lambda_i = \left(\frac{a_i}{r_i} \right) D_i, \quad \text{where } r_i = (m_i - D_i).$$

λ_i may be regarded as the critical amount of resource needed by the predator to just survive in the absence of competition.

If n species are competing for a single, limiting resource that is supplied at a constant rate, the species with the smallest λ wins the competition and all other species go extinct [7]. The surviving species and the "prey" approach constant values; there is no limiting periodic behavior.

When the resource is allowed to regenerate logistically and the consumers also have saturating functional responses, the possible outcomes are increased to include periodic solutions and dynamic coexistence between predators [8], [9].

In this paper we examined cases in which the predator λ 's are sufficient for neither or only one predator to survive on the prey population. The most important new result, however, comes from the case in which both predators can survive handily when grown alone on the prey. This condition is met when the λ parameters for both predators are less than K , the carrying capacity of the prey, and the maximal intrinsic rate of increase for both predators is positive. We prove that predator 1 outcompetes predator 2 (which dies out) when $\lambda_1 < \lambda_2$ and $m_1/D_1 \geq m_2/D_2$. When these conditions are violated, coexistence of the predators is possible as illustrated by the numerical results in [8].

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