Two Predators Competing for Two Prey Species:
An Analysis of MacArthur's Model

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ABSTRACT

This paper concerns the exploitative competition of two predators for two prey species. We analyze the model proposed by MacArthur with more general parameters. MacArthur used the model to address questions of species packing on resources, but he did not completely determine analytically under what conditions will neither, one, or both predator species and one or both prey species, survive. Our analysis is global for all cases except one, for which we performed a numerical analysis. We conclude that the behavior of this predator-prey system is more complicated than previously thought. In particular, we analyze cases in which the two-predator, two-prey system catastrophically collapses to a one-predator, two-prey system, or even to one-predator, one-prey system. We also show that there are cases in which the initial numbers of the two predators determine the pattern of this collapse. These conclusions suggest that caution should be exercised in interpreting any conclusions of species packing that are based solely upon a graphical analysis of the MacArthur model.

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1. INTRODUCTION

In 1972 MacArthur [9] introduced a model of two "consumer" species, x_1 and x_2, competing for food on shared "resources," R_1 and R_2. Because he assumed that the "resources" were capable of self-reproduction and regenerated logistically in the absence of consumption, the model is perhaps

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more appropriately treated as a case of competing predators sharing two prey species. MacArthur did little formal analysis of this model system before his untimely death. This paper is a rigorous analysis of the global behavior of MacArthur's two-predator, two-prey model. The principal result of the paper is to define the conditions under which the competing predator species survive or die out. To our knowledge, no such analysis has yet appeared in the literature.

MacArthur's model represents a major advance in biological realism over classical mathematical treatments of competing species because it incorporates explicit equations for the dynamics of the limiting resources (i.e., prey) in addition to the usual equations for each competitor. However, the added realism markedly increased the complexity of the analytical problem because of the jump from the classical two-dimensional system to a four-dimensional system. Perhaps because the increased difficulties of the four-dimensional system were enough, MacArthur apparently chose to model only the simplest possible predator functional response to increasing prey density. This is the response in which the predator's feeding rate increases linearly with prey density (type I response under Holling's [3] classification). This mass-action formulation of feeding rate characterizes the classical models of predator-prey interaction [11], and is most accurate at low prey densities. We report elsewhere [5] on the consequences of incorporating nonlinear functional responses that saturate at some maximal feeding rate as the prey density becomes sufficiently large.

The remainder of this paper is organized as follows. A statement of the model and definitions of its parameters appear in Sec. 2. The analytical results are given without proof in Sec. 3. The proofs are deferred to the appendix. Finally, in Sec. 4 the results are discussed in biological terms and compared with the earlier partial results of MacArthur [9].

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 two prey species, R_1 and R_2. We specifically assume that the predator species compete purely exploitatively, with no interference between rivals. Both species have access to prey and compete only be lowering the population of shared prey. Death rates are assumed to follow a "type III" survivorship [10] in which 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 is linear. With these assumptions the

model is given by

$$R_1' = R_1\left[r_1\left(1 - \frac{R_1}{K_1}\right) - k_{11}x_1 - k_{21}x_2\right],$$

$$R_2' = R_2\left[r_2\left(1 - \frac{R_2}{K_2}\right) - k_{12}x_1 - k_{22}x_2\right],$$

$$x_1' = x_1[b_{11}R_1 + b_{12}R_2 - D_1] \tag{2.1}$$

$$x_2' = x_2[b_{21}R_1 + b_{22}R_2 - D_2],$$

$$R_i(0) > 0, \quad x_i(0) > 0 \quad \text{for} \quad i = 1, 2,$$

where

$' = d/dt$,

$t =$ time,

$R_i(t) =$ the number of ith prey at time t,

$x_i(t) =$ the number of ith predator at time t,

$r_i =$ the intrinsic rate of increase for ith prey,

$K_i =$ the carrying capacity for ith prey,

$b_{ij} =$ the birth rate per predator (predator species i) per unit prey (prey species j) consumed,

$k_{ij} =$ the feeding rate per predator (predator species i) per unit prey (prey species j) consumed,

$D_i =$ the death rate of ith predator.

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 or die out? If only one predator survives, we also seek to determine the limiting behavior of the surviving predator and its prey.

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 appendix. The first lemma is a statement that the system given by (2.1) is as "well behaved" as one intuits from the biological problem. The proof of the lemma is easy and we omit it.

LEMMA 3.1

Solutions of (2.1) are positive and bounded. Furthermore, for any $\varepsilon > 0$ there exists $t_0 > 0$ such that $R_i(t) < K_i + \varepsilon$ for $t > t_0$, $i = 1, 2$.

The next lemma provides conditions under which the predators cannot survive on the prey given the carrying capacity of each prey population even in the absence of competition:

LEMMA 3.2

A necessary condition for either predator species x_i to survive is $b_{i1}K_1 + b_{i2}K_2 > D_i$.

This lemma states that if the death rate D_i for the ith predator is too high or if the carrying capacities K_1 and K_2 for the prey species are collectively too small, then the ith predator will die out. We note the result is independent of competition.

We state the principal result in the case of inadequate carrying capacities of preys in seven parts. We are able in Theorem 3.3 to determine the globally asymptotic behavior of the solutions. The theorem may be summarized by noting that the unsuccessful competitor does not affect the eventual behavior of the survivor and its prey.

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

THEOREM 3.3(i)

If $b_{i1}K_2 + b_{i1}K_2 < D_i$ for $i = 1, 2$, then

$$\lim_{t \to \infty} R_i(t) = K_i,$$

$$\lim_{t \to \infty} x_i(t) = 0, \qquad i = 1, 2.$$

We note that Theorem 3.3(i) simply follows from Lemma 3.2 and (2.1).
Let $\lambda_{ij} = D_i / b_{ij}$, $i, j = 1, 2$.

THEOREM 3.3(ii)

Let $b_{11}K_1 + b_{12}K_2 > D_1$ and $b_{21}K_1 + b_{22}K_2 < D_2$. If

$$0 < \frac{k_{11}}{r_1(1 - \lambda_{11}/K_1)} < \frac{k_{12}}{r_2}, \tag{A1}$$

then

(C1) *the trajectory of (2.1) approaches the equilibrium (E_{11}) as $t \to \infty$, where*

$$(E_{11}) = (\bar{R}_1, 0, \bar{x}_1, 0),$$

and

$$\tilde{R}_1 = \lambda_{11}, \qquad \tilde{x}_1 = \frac{r_1}{k_{11}}\left(1 - \frac{\lambda_{11}}{k_1}\right).$$

THEOREM 3.3(iii)

Let $b_{11}K_1 + b_{12}K_2 > D_1$ and $b_{21}K_1 + b_{22}K_2 < D_2$. If

$$0 < \frac{K_{12}}{r_2(1 - \lambda_{12}/K_2)} < \frac{k_{11}}{r_1}, \qquad (A2)$$

then

(C2) the trajectory of (2.1) approaches the equilibrium (E_{12}) as $t \to \infty$, where

$$(E_{12}) = (0, \tilde{R}_2, \tilde{x}_1, 0),$$

and

$$\tilde{R}_2 = \lambda_{12}, \qquad \tilde{x}_1 = \frac{\gamma_2}{k_{12}}\left(1 - \frac{\lambda_{12}}{K_2}\right).$$

THEOREM 3.3(iv)

Let $b_{11}K_1 + b_{12}K_2 > D_1$ and $b_{21}K_1 + b_{22}K_2 < D_1$. If

$$\frac{k_{12}}{r_2}\left(1 - \frac{\lambda_{11}}{K_1}\right) < \frac{k_{11}}{r_1} \quad and \quad \frac{k_{11}}{r_1}\left(1 - \frac{\lambda_{12}}{K_2}\right) < \frac{k_{12}}{r_2}, \qquad (A3)$$

then

(C3) the trajectory of (2.1) approaches the equilibrium (E_{13}) as $t \to \infty$, where

$$(E_{13}) = (R_{11}^*, R_{12}^*, x_1^*, 0),$$

$$R_{11}^* = \frac{b_{12}}{\dfrac{r_1}{k_{11}}\dfrac{b_{12}}{K_1} + \dfrac{r_2}{k_{12}}\dfrac{b_{11}}{K}}\left(\frac{r_1}{k_{11}} - \frac{r_2}{k_{12}}\left(1 - \frac{\lambda_{12}}{K_2}\right)\right) < K_1$$

$$R_{12}^* = \frac{b_{11}}{\dfrac{r_1}{k_{11}}\dfrac{b_{12}}{K_1} + \dfrac{r_2}{k_{12}}\dfrac{b_{11}}{K_2}}\left(\frac{r_2}{k_{12}} - \frac{r_1}{k_{11}}\left(1 - \frac{\lambda_{11}}{K_1}\right)\right) < K_2$$

$$x_1^* = \frac{r_1}{k_{11}}\left(1 - \frac{R_{11}^*}{K_1}\right) = \frac{r_2}{k_{12}}\left(1 - \frac{R_{12}^*}{K_2}\right).$$

We note that it is impossible that

$$\frac{k_{11}}{r_1} > \frac{k_{12}}{r_2(1-\lambda_{12}/K_2)} > 0 \quad \text{and} \quad \frac{k_{12}}{r_2} > \frac{k_{11}}{r_1(1-\lambda_{11}/K_1)} > 0$$

hold simultaneously. We also note that K_1 may be less than λ_{11} and K_2 may be less than λ_{12} in (A3).

Similarly we have

THEOREM 3.3(v)

Let $b_{11}K_1 + b_{12}K_2 < D_1$ and $b_{21}K_1 + b_{12}K_2 > D_2$. If

$$0 < \frac{k_{21}}{r_1\left(1-\dfrac{\lambda_{21}}{K_1}\right)} < \frac{k_{22}}{r_2}, \qquad (B1)$$

then

(C4) *the trajectory of (2.1) approaches the equilibrium* (E_{21}) *as* $t \to \infty$, *where*

$$(E_{21}) = (\underline{R}_1, 0, 0, \underline{x}_2)$$

and

$$\underline{R}_1 = \lambda_{21}, \qquad \underline{x}_2 = \frac{r_1}{k_{21}}\left(1-\frac{\lambda_{21}}{K_1}\right).$$

THEOREM 3.3(vi)

Let $b_{11}K_1 + b_{12}K_2 < D_1$ and $b_{21}K_1 + b_{22}K_2 > D_2$. If

$$0 < \frac{k_{22}}{r_2(1-\lambda_{22}/K_2)} > \frac{k_{21}}{r_1}, \qquad (B2)$$

then

(C5) *the trajectory of (2.1) approaches the equilibrium* (E_{22}) *as* $t \to \infty$, *where*

$$(E_{22}) = (0, \underline{R}_2, 0, \underline{x}_2)$$

and

$$\underline{R}_2 = \lambda_{22}, \qquad \underline{x}_2 = \frac{r_2}{k_{22}}\left(1-\frac{\lambda_{22}}{K_2}\right).$$

THEOREM 3.3(vii)

Let $b_{11}K_1 + b_{12}K_2 < D_1$ and $b_{21}K_1 + b_{22}K_2 > D_2$. If

$$\frac{k_{22}}{r_2}\left(1 - \frac{\lambda_{21}}{K_1}\right) < \frac{k_{21}}{r_1} \quad and \quad \frac{k_{21}}{r_1}\left(1 - \frac{k_{22}}{K_2}\right) < \frac{k_{22}}{r_2}, \qquad (B3)$$

then

(C6) the trajectory of (2.1) approaches the equilibrium (E_{23}) as $t \to \infty$, where,

$$(E_{23}) = (R_{21}^*, R_{22}^*, 0, x_2^*),$$

$$R_{21}^* = \frac{b_{22}}{\frac{r_1}{k_{21}}\frac{b_{22}}{K_1} + \frac{r_2}{k_{22}}\frac{b_{21}}{K_2}}\left[\frac{r_1}{k_{21}} - \frac{r_2}{k_{22}}\left(1 - \frac{\lambda_{22}}{K_2}\right)\right] < K_1,$$

$$R_{22}^* = \frac{b_{21}}{\frac{r_1}{k_{21}}\frac{b_{22}}{K_1} + \frac{r_2}{k_{22}}\frac{b_{21}}{K_2}}\left[\frac{r_2}{k_{22}} - \frac{r_1}{k_{21}}\left(1 - \frac{\lambda_{21}}{K_1}\right)\right] < K_2,$$

$$x_2^* = \frac{r_1}{k_{21}}\left(1 - \frac{R_{21}^*}{K_1}\right) = \frac{r_2}{k_{22}}\left(1 - \frac{R_{22}^*}{K_2}\right).$$

In order to discuss the interior equilibrium point, we may assume as a basic hypothesis:

(H1) $b_{i1}K_1 + b_{i2}K_2 > D_i$ for $i = 1, 2$.

Under the assumption (H1), the equations of (2.1) may be relabeled without loss of generality, so that we assume either

(H2) $\lambda_{11} < \lambda_{21}, \ \lambda_{12} < \lambda_{22}$

or

(H3) $\lambda_{11} < \lambda_{21}, \ \lambda_{22} < \lambda_{12}$.

We note that most of the conditions on parameters for the various cases in Theorems 3.3, 3.4, 3.5, 3.9 can also be established by the linearization method.
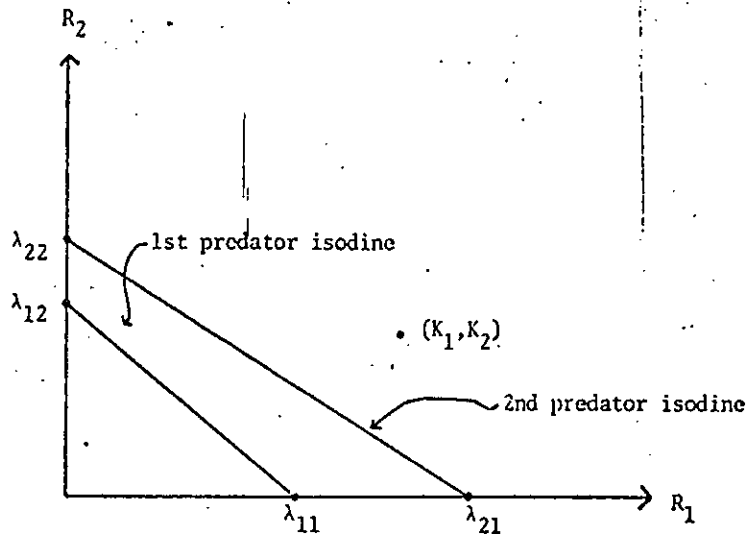
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FIGURE 1.

THEOREM 3.4

Let (H1) and (H2) hold (see Fig. 1). Then the statements in Theorem 3.3 (ii), (iii), (iv) hold.

THEOREM 3.5

Assume (H1) and (H3) hold. Let

$$R_{1c}^* = \frac{D_1 b_{22} - D_2 b_{12}}{b_{11} b_{22} - b_{12} b_{21}}$$

and

$$R_{2c}^* = \frac{D_2 b_{11} - D_1 b_{21}}{b_{11} b_{22} - b_{12} b_{21}}.$$

(i) If $K_1 > R_{1c}^*$ and $K_2 < R_{2c}^*$ [see Fig. 2(a)], then the statements in Theorem 3.3(ii), (iv) hold.

(ii) If $K_1 < R_{1c}^*$ and $K_2 > R_{2c}^*$ [see Fig. 2(b)], then the statements in Theorem 3.3(vi), (vii) hold.

Remark. From Fig. 2(a), the assumption (A2) in Theorem 3.3(iii) doesn't hold. Similarly from Fig. 2(b), the assumption (B1) in Theorem 3.3(v) doesn't hold.
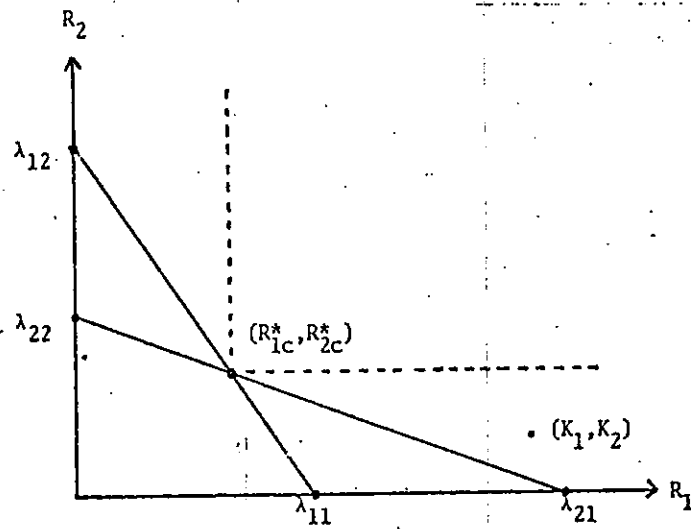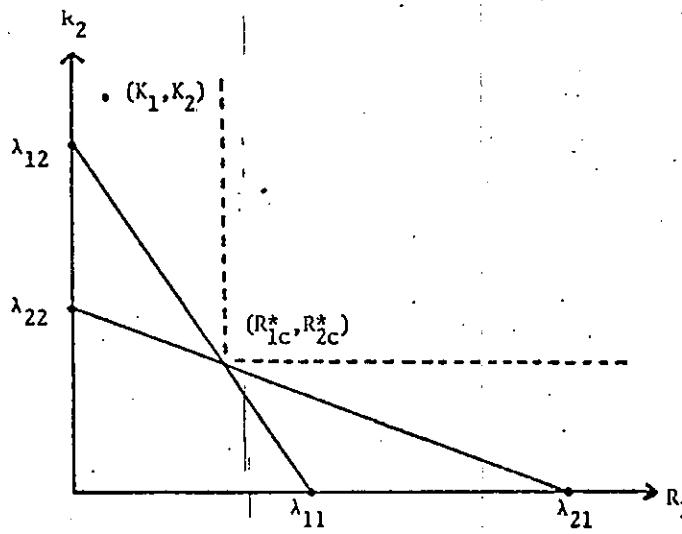
MACARTHUR'S MODEL

FIGURE 2a.

FIGURE 2b.

For the rest of this section we assume

(H4) $K_1 > R_{1c}^*$ and $K_2 > R_{2c}^*$.

We note the following lemmas.

LEMMA 3.6

Let

$$P_{11} = \frac{k_{11}}{r_1(1 - R_{1c}^*/K_1)}, \qquad P_{12} = \frac{k_{12}}{r_2(1 - R_{2c}^*/K_2)},$$

$$P_{21} = \frac{k_{21}}{r_1(1 - R_{1c}^*/K_1)}, \qquad P_{22} = \frac{k_{22}}{r_2(1 - R_{2c}^*/K_2)},$$

$$C_1 = \frac{k_{11}}{k_{12}} \qquad C_2 = \frac{k_{21}}{k_{22}},$$

$$x_{1c}^* = \frac{r_1 k_{22}(1 - R_{1c}^*/K_1) - r_2 k_{21}(1 - R_{2c}^*/K_2)}{k_{11}k_{22} - k_{12}k_{21}},$$

$$x_{2c}^* = \frac{r_2 k_{11}(1 - R_{2c}^*/K_2) - r_1 k_{12}(1 - R_{1c}^*/K_1)}{k_{11}k_{22} - k_{12}k_{21}}.$$

(i) The "positive" equilibrium $(E_c) = (R_{1c}^*, R_{2c}^*, x_{1c}^*, x_{2c}^*)$ exists if and only if $P_{11} > P_{12}$, $P_{22} > P_{21}$ or $P_{11} < P_{12}$, $P_{22} < P_{21}$.

(iii) Under assumptions (H1), (H3), and (H4), a necessary condition for the asymptotic stability of the equilibrium (E_c) is $C_1 > C_2$.

(iii) If $C_2 > C_1$, then (E_c) is an unstable saddle point. We note that it is hard to verify (E_c) is asymptotically stable, as the reader can see in the proof of (ii).

Remark 1. P_{ij} is the predation intensity exerted by the ith predator on the jth prey species at equilibrium.

·LEMMA 3.7

Let (H1), (H3), and (H4) hold. Then

(i) $R_{11}^* < R_{1c}^*$ iff $P_{12} < P_{11}$.
(ii) $R_{21}^* < R_{1c}^*$ iff $P_{22} < P_{21}$.

Remark 2. Lemma 3.7 is very useful in graphing so that we can determine the stability of the equilibria.

LEMMA 3.8

Let (H1), (H3), and (H4) hold.

(i) If $P_{22} > P_{21}$, $P_{12} > P_{11}$, then $\lim_{t \to \infty} R_2(t) x_2(t) = 0$.
(ii) If $P_{21} > P_{22}$, $P_{11} > P_{12}$, the $\lim_{t \to \infty} R_1(t) x_1(t) = 0$.
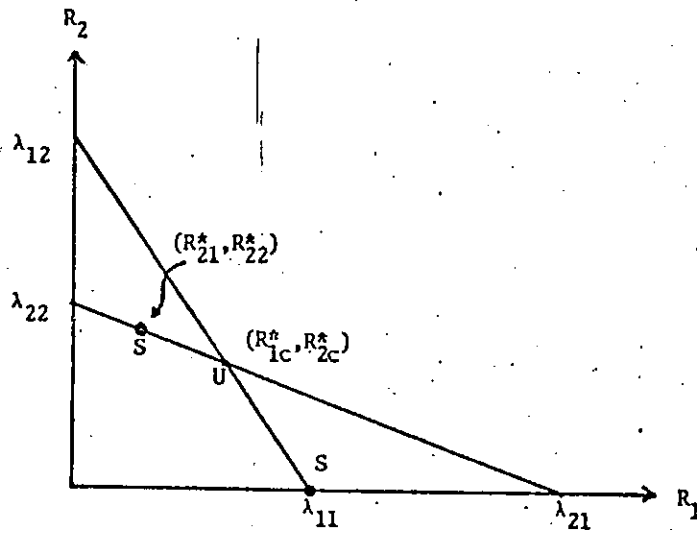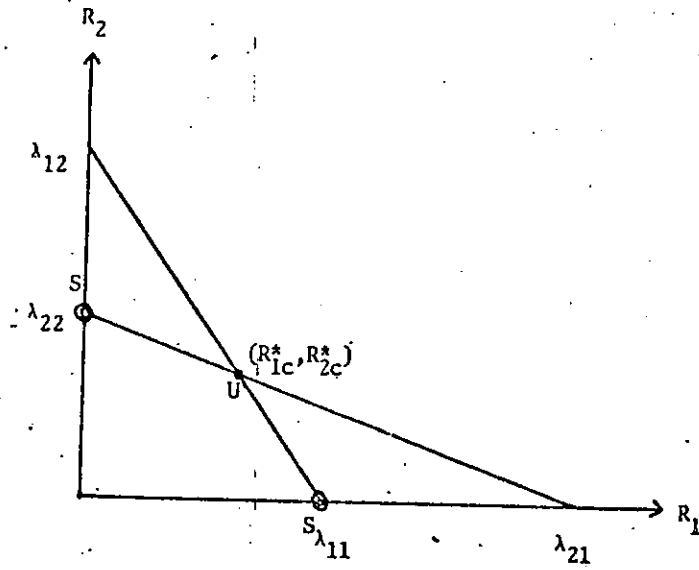
FIG. 3. S means that the equilibrium is stable; U means that the equilibrium is unstable.

MacARTHUR'S MODEL

R_2

λ_{12}

S

λ_{22}

U (R^*_{1c}, R^*_{2c})

E_c

(R^*_{11}, R^*_{12}) • S

λ_{11} λ_{21} R_1

X_2

λ_{12}

λ_{22}

S

(R^*_{21}, R^*_{22}) E_c

(R^*_{1c}, R^*_{2c})

U

• S

(R^*_{11}, R^*_{12})

λ_{11} λ_{21} X_1

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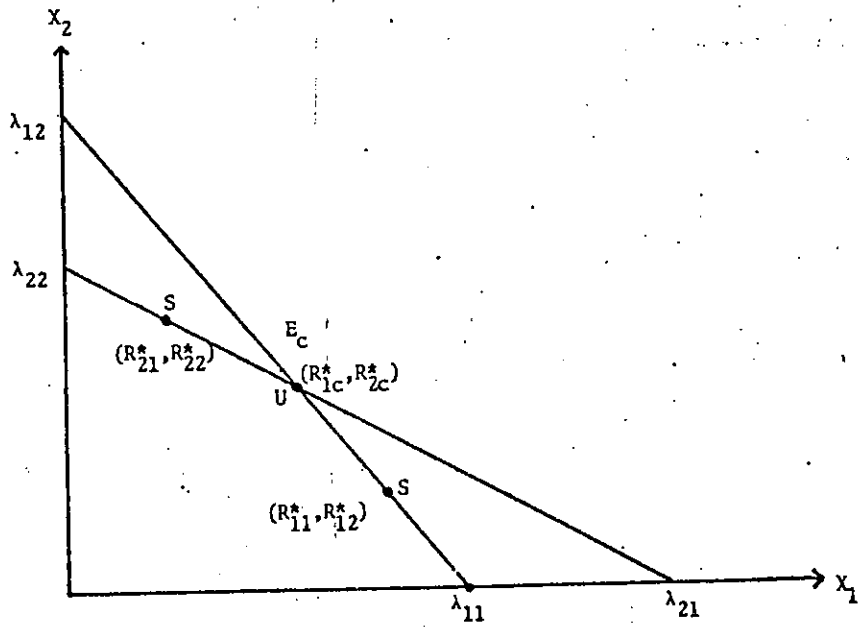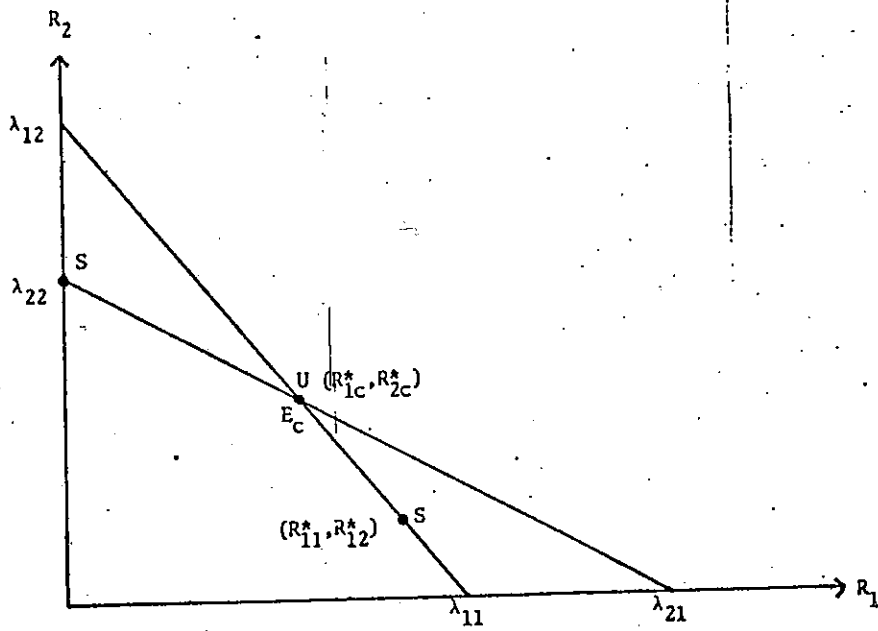
4. DISCUSSION

This paper is a mathematical analysis of the behavior of a model of two predator species competing exploitatively for two prey species. Each prey species grows logistically in the absence of predation, and the predator species consume the prey according to a linear functional response. The prey can be regarded as "substitutable" resources from the perspective of the predators, since the "indifference" curves of equal growth rates arise as constant linear combinations of densities of the two prey species [7].

The outcome of competition depends on the prey parameters r_j and K_j (the intrinsic rate of increase and carrying capacity of the jth prey species, respectively), as well as on the birth, death, and feeding rates (b_{ij}, D_i, k_{ij}) of the ith predator species. Particularly important composite parameters are λ_{ij} and P_{ij}. In this model λ_{ij} is the ratio of the ith predator's specific death rate to its specific birth rate on the jth resource per unit prey consumed $(\lambda_{ij} = D_i/b_{ij})$. λ has units of prey density because the units of D are predator^{-1}time^{-1}, whereas the units of b are prey^{-1}predator^{-1}time^{-1}. λ_{ij} represents the density of prey species j at which predator i's birth rate just equals its death rate. We will cal λ_{ij} the "subsistence density" of prey j minimally necessary to support predator i. The second composite parameter, P_{ij}, is the predation intensity exerted by the ith predator on the jth prey species at equilibrium. Predation intensity is defined as the ratio of the per capita (per prey, per predator) consumption rate of prey divided by the per capita (per prey) rate of increase of the prey.

Elsewhere it has been shown that if n predator species are competing for a single prey species which grows logistically, and if the predators consume prey according to a linear functional response, then only one predator species will survive in the end, that being the species with the smallest λ. The surviving predator and its prey approach constant values (see [4], [8]).

When a second prey species is added to the system, the possible outcomes are more numerous. In this paper we consider only the two-predator case. The focus of the analysis has been to define the analytic conditions under which neither, one, or both predator species survive. Given that both prey and both predators are present at the beginning, there are eight equilibria which can be reached by (2.1) (Table 1). Each of these equilibria can arise in several different ways, which we have classified (Table 2). We have divided our results into three general cases:

Case I: neither predator can survive, even without competition;

Case II: one predator can survive on these prey species, but the other cannot;

Case III: both predators can survive on these prey, at least in the absence of competition.

TABLE 1

Biological (Nonnegative) Equilibria of (2.1)

	Equilibrium	Refer to Theorem
1.	$(R_1, R_2, 0, 0)$	3.3(i)
2.	$(R_1, 0, x_1, 0)$	3.3(ii)
3.	$(0, R_2, x_1, 0)$	3.3(iii)
4.	$(R_1, R_2, x_1, 0)$	3.3(iv)
5.	$(R_1, 0, 0, x_2)$	3.3(v)
6.	$(0, R_2, 0, x_2)$	3.3(vi)
7.	$(R_1, R_2, 0, x_2)$	3.3(vii)
8.	(R_1, R_2, x_1, x_2)	3.9
9.	$(0, 0, 0, 0)$	Impossible[a]
10.	$(R_1, 0, 0, 0)$	Impossible[a]
11.	$(0, R_2, 0, 0)$	Impossible[a]
12.	$(0, 0, x_1, 0)$	Impossible, 3.3(i)
13.	$(0, 0, 0, x_2)$	Impossible, 3.3(i)
14.	$(0, 0, x_1, x_2)$	Impossible, 3.3(i)
15.	$(R_1, 0, x_1, x_2)$	Impossible; cf. [4]
16.	$(0, R_2, x_1, x_2)$	Impossible; cf. [4]

[a]Only equilibrium points 1–8 are possible given the initial conditions in (2.1), namely, $R_1(0)$, $R_2(0)$, $x_1(0), x_2(0) > 0$.

Cases II and III have several subcases with different biological outcomes (Table 2).

CASE I

This represents the case in which neither predator can survive on the prey species, regardless of the presence or absence of its rival. This situation arises when the carrying capacities of the prey species are collectively too small to support either predator [Theorem 3.3(i)]. When both predators go extinct, each prey species equilibrates at its carrying capacity. This occurs when $b_{i1}K_1 + b_{i2}K_2 < D_i$ for $i = 1, 2$ predators.

CASE II

This case is partially understandable from the outcome in Case I, since one of the predators cannot survive on the prey no matter what its rival does, but the rival can survive when grown alone. In the limit this case goes to a two-prey, one-predator system, or sometimes to a one-prey, one-predator system, whose behavior is easy to understand if we apply Liapunov's function in (5.2), (5.3), (5.4) without δx_2.

TABLE 2

Detailed Classification of Outcomes

	Predator		Prey	
	x_1	x_2	R_1	R_2

I. When grown alone neither predator survives.

$b_{11}K_1 + b_{12}K_2 < D_1$ and $b_{21}K_1 + b_{22}K_2 < D_2$

x_1	x_2	R_1	R_2
0	0	K_1	K_2

II. When grown alone, only one predator survives.

A. $b_{11}K_1 + b_{12}K_2 > D_1$ and $b_{21}K_1 + b_{22}K_2 < D_2$

1. $0 < \dfrac{k_{11}}{r_1(1-\lambda_{11}/K_1)} < \dfrac{k_{12}}{r_2}$

x_1	x_2	R_1	R_2
$\dfrac{r_1}{k_{11}}(1-\dfrac{\lambda_{11}}{K_1})$	0	λ_{11}	0

2. $0 < \dfrac{k_{12}}{r_2(1-\lambda_{12}/K_2)} < \dfrac{k_{11}}{r_1}$

x_1	x_2	R_1	R_2
$\dfrac{r_2}{k_{12}}(1-\dfrac{\lambda_{12}}{K_2})$	0	0	λ_{12}

3.* $\dfrac{k_{12}}{r_2}(1-\dfrac{\lambda_{11}}{K_1}) < \dfrac{k_{11}}{r_1}$ and

$\dfrac{k_{12}}{r_1}(1-\dfrac{\lambda_{12}}{K_2}) < \dfrac{k_{12}}{r_2}$

x_1	x_2	R_1	R_2
x_1^*	0	R_{11}^*	R_{12}^*

B. $b_{11}K_1 + b_{12}K_2 < D_1$ and $b_{21}K_1 + b_{22}K_2 > D_2$

1. $0 < \dfrac{k_{21}}{r_1(1-\lambda_{21}/K_1)} < \dfrac{k_{22}}{r_2}$

x_1	x_2	R_1	R_2
0	$\dfrac{r_1}{k_{21}}(1-\dfrac{\lambda_{21}}{K_1})$	λ_{21}	0

2. $0 < \dfrac{k_{22}}{r_2(1-\lambda_{22}/K_2)} < \dfrac{k_{21}}{r_1}$

x_1	x_2	R_1	R_2
0	$\dfrac{r_2}{k_{22}}(1-\dfrac{\lambda_{22}}{K_2})$	0	λ_{22}

3.* $\dfrac{k_{22}}{r_2}(1-\dfrac{\lambda_{21}}{K_1}) < \dfrac{k_{21}}{r_1}$

$\dfrac{k_{11}}{r_1}(1-\dfrac{\lambda_{22}}{K_2}) < \dfrac{k_{22}}{r_2}$

x_1	x_2	R_1	R_2
0	x_2^*	R_{21}^*	R_{22}^*

III. Both predators can survive when grown alone.

$b_{11}K_1 + b_{12}K_2 > D_1$ and $b_{21}K_1 + b_{22}K_2 > D_2$

A. $\lambda_{11} < \lambda_{21}, \lambda_{12} < \lambda_{22}$

  1. Same as Case IIA1

  2. Same as Case IIA2

  3. Same as Case IIA3

B. $\lambda_{21} < \lambda_{11}, \lambda_{22} < \lambda_{12}$

  1. Same as Case IIB1

  2. Same as Case IIB2

  3. Same as Case IIB3

C. $\lambda_{11} < \lambda_{21}, \lambda_{22} < \lambda_{12}$

  1. $K_1 > R_{1c}^*, K_2 < R_{2c}^*$

    a. Same as Case IIA1

    b. Same as Case IIA3

/ 6

2. $K_1 < R_{1c}^*, K_2 > R_{2c}^*$

    a. Same as Case IIB2
    b. Same as Case IIB3

3. $K_1 > R_{1c}^*, K_2 > R_{2c}^*$

    a. $P_{22} > P_{21}, P_{12} > P_{11}$
       1. Same as Case IIA1
       2. Same as Case IIA3
    b. $P_{22} > P_{21}, \quad P_{11} > P_{12} x_{1c}^* x_{2c}^* R_{1c}^* R_{2c}^*$
    c. $P_{21} >$
       1. Same as Case IIB2
       2. Same as Case IIB3
    d. $P_{21} > P_{22}, P_{12} > P_{11}$, outcomes depends on initial conditions
       1. Same as IIIC but interchange subscripts 1 and 2

*Incomplete results checked by numerical simulation.

Suppose predator x_1 survives and predator x_2 dies out. Then there are three outcomes possible depending on the survival of the prey species:

Case IIA1: R_1 survives, R_2 dies out;
Case IIA2: R_1 dies out, R_2 survives, and
Case IIA3: R_1 and R_2 both survive.

The parallel cases IIB1, IIB2, and IIB3 also exist, in which predator x_2 survives and predator x_1 dies out. MacArthur [9] made no mention of the possibility of Cases IIA1,2 and IIB1,2, and apparently was unaware of their existence.

However, these cases are of considerable ecological interest because they imply catastrophic change in the community as a result of interactions of member species. Thus, it is relevant to consider the biological circumstances under which the two-predator, two-prey system collapses to a one-predator, one-prey system. Again, consider the case in which predator x_2 dies out because of insufficient prey carrying capacity, but x_1 can survive. In case IIA1, when the inequalities

$$\frac{k_{11}}{r_1} < \frac{k_{12}}{(1 - \lambda_{12}/K_2)} = P_{12} \quad \text{and} \quad \frac{k_{12}}{r_2} > \frac{k_{11}}{r_1(1 - \lambda_{11}/K_1)} = P_{11}$$

are satisfied, prey species R_2 is consumed to extinction by the surviving predator x_1, and x_1 and R_1 approach equilibrium values.

The above inequalities in biological terms compare the two prey species in terms of the intensity of predation they experience on a per capita basis, relative to the per capita power of each prey species to multiply. High k_{ij}/r_j ratios reflect a high predation intensity on the basis of prey per capita

growth rate. Thus, for a given consumption rate, a lower rate of prey increase results in a higher steady-state predation intensity. Together the inequalities above state that predation intensity in terms of specific rate of consumption per unit specific rate of prey increase is always greater for prey species R_2 than for prey species R_1 at all prey densities. Moreover, even when R_2 is at very low density and regenerating at its maximal, density-independent rate, it still experiences a higher per capita predation intensity, k_{12}/r_2, than prey species R_1 does. This is in spite of the fact that R_1 is at higher density and is regenerating at a submaximal, density-dependent rate under steady-state predation, $k_{11}/r_1(1-\lambda_{11}/K)$. A symmetrical biological interpretation exists for Case IIA2, in which prey species R_2 survives and R_1 dies out from predation.

In Case IIA3 both prey species survive under predation from x_1. The reason both species persist is that predation pressures are balanced. Each prey species at low density sustains a lower predation intensity than the other prey species sustains at its equilibrium density under steady-state predation. This is stated mathematically by the inequalities

$$\frac{k_{11}}{r_1} < \frac{k_{12}}{r_2(1-\lambda_{12}/K_2)} = P_{12} \quad \text{and} \quad \frac{k_{12}}{r_2} < \frac{k_{11}}{r_1(1-\lambda_{11}/K_1)} = P_{11}.$$

This balancing "frequency dependence" in predation intensity maintains both prey species in the system. When both prey species are individually inadequate to support the predator ($\lambda_{1j} > K_j$), but are adequate as a food supply when taken together, then the above inequalities are written as

$$\frac{k_{12}}{r_1}\left(1-\frac{\lambda_{12}}{K_2}\right) < \frac{k_{12}}{r_2} \quad \text{and} \quad \frac{k_{12}}{r_2}\left(1-\frac{\lambda_{11}}{K_1}\right) < \frac{k_{11}}{r_1}.$$

On a mathematical note, although the behavior of the two-prey, one-predator system is readily understood, it is technically quite difficult to show the results in Theorem 3.3(ii), (iii), and (iv). In this article, we consider only trajectories which begin in the positive orthant. In [2] Goh studied the behavior of a boundary equilibrium by the technique of sector stability. In that case, the considered trajectories begin in the nonnegative orthant.

CASE III

This case represents the most interesting and potentially the most complex situation of the two-predator, two-prey system. In this case, both species can survive handily when grown alone without competition on the prey species. This condition is met when the prey carrying capacities are large enough that $b_{i1}K_1 + b_{i2}K_2 > D_i$ for both predators ($i=1,2$). In this case there are four different possible biological outcomes of competition, which

parallel the cases from classical Lotka-Volterra theory (11). These cases are: (1) predator x_1 always eliminates predator x_2; (2) predator x_2 always eliminates predator x_1; (3) predators x_1 and x_2 coexist in stable equilibrium; or (4) predators x_1 and x_2 coexist unstably, with the usual result that one species eliminates the other, depending on initial density.

Each of these biological outcomes, it turns out, can arise in a number of mechanistically different ways under Case III. For example, under Case IIIA predator x_1 always eliminates predator x_2. However, this outcome also occurs if the conditions for Cases IIIC1 or IIID2 are met, and can occur when cases IIIC3 and IIID3 hold (Table 2). Case IIIA represents the situation in which predator x_2 has the smaller λ with respect to each prey species, i.e., $\lambda_{11} < \lambda_{21}$ and $\lambda_{12} < \lambda_{22}$. In this case x_1 is a clear winner, because it can persist at lower prey densities on either prey species than predator x_2 can. However, in Case IIIC predator x_1 only has the smaller λ for prey species R_1; predator x_2 is better on prey R_2 than x_1 is. In this case, predator x_1 will always win when there is not enough R_2 available (K_2 is too small) to support predator x_2 in the face of rival predation on R_2 from predator x_1. Case IIIC1 defines the conditions under which the carrying capacity of prey species R_2 is too low for predator x_2 to survive in the face of competing predation on its principal prey (Table 2).

In Case IIIC3 the carrying capacities of the two prey species are adequate for the predators, so the outcome depends in this case on the relative predation intensities imposed on the two prey species by the two predator species. If these predation intensities are balanced, the predators can coexist stably [Case IIIC3a(2), Table 2]. If they are unbalanced, one or the other predator species is eliminated.

The complete list of biological conditions for stable coexistence between the two predator species in this model can be stated as follows:

(1) Each predator must be capable of persisting on the prey when grown without competition (Case III).

(2) Each predator must have the lower subsistence density of prey (lower λ) for one of the prey species (Case IIIC or IIID). (If one of the predators has lower λ's for both prey species, it will eliminate its rival.)

(3) There must be sufficient prey of both species (adequate prey carrying capacity) to support each predator species given steady-state predation. (Adequacy of prey carrying capacity is defined in Cases IIIC3 and IIID3.)

(4) Finally, the predation intensity imposed by each predator species on each prey species must be greater on that prey species for which the predator has the lower λ [Cases IIIC3a(2) and IIID3a(2)].

Mathematically, condition (4) for coexistence can be written as follows. If $\lambda_{11} < \lambda_{21}$ and $\lambda_{22} < \lambda_{12}$, then given conditions (1) and (3), the condition for

stable coexistence in terms of predation intensity is that $P_{11} > P_{12}$ and $P_{22} > P_{21}$, or that

$$\frac{k_{11}}{r_1(1 - R^*_{1c}/K_1)} > \frac{k_{12}}{r_2(1 - R^*_{2c}/K_2)} \quad \text{and} \quad \frac{k_{22}}{r_2(1 - R^*_{2c}/K_2)} > \frac{k_{21}}{r_1(1 - R^*_{1c}/K_1)}.$$

Thus, predator x_1 has the lower λ on R_1, predator x_2 has the lower λ on R_2, and the predation intensities of x_1 and x_2 are greater on R_1 and R_2, respectively. In terms of the composite parameters, these inequalities reduce to the condition $P_{11} > P_{12}$, $P_{22} > P_{21}$ for $\lambda_{11} < \lambda_{21}$ and $\lambda_{22} < \lambda_{12}$. By symmetry, stable coexistence also occurs when $P_{11} < P_{12}$, $P_{22} < P_{21}$ if $\lambda_{21} < \lambda_{11}$ and $\lambda_{12} < \lambda_{22}$. Condition (4) for the coexistence of two species competing exploitatively for two resources which regenerate at a constant rate has also been reported in [5] and [7].

Initial densities of the rival predator species influence the outcome of competition when each predator imposes its more intense predation pressure on the primary prey species of its rival, i.e., the prey species for which the rival predator has a lower λ. In this case, the initial numbers of each predator will determine the eventual winner. Mathematically, this condition is given by $P_{11} < P_{12}$ and $P_{22} < P_{21}$, or

$$\frac{k_{11}}{r_1(1 - R^*_{1c}/K_1)} < \frac{k_{12}}{r_2(1 - R^*_{2c}/K_2)} \quad \text{and} \quad \frac{k_{22}}{r_2(1 - R^*_{2c}/K_2)} < \frac{k_{21}}{r_1(1 - R^*_{1c}/K_1)},$$

when $\lambda_{11} < \lambda_{21}$ and $\lambda_{22} < \lambda_{12}$ [case IIIC3b(2)].

We note that proof of Theorem 3.9 is still incomplete. However, from the numerous partial results on the theorem, supplemented by numerical analysis where needed, we can be certain of the validity of the conclusions under (H1), (H3), and (H4).

In its original form as presented by MacArthur [9], the two-predator, two-prey model is a special case of the model we have analyzed here. In that form, he set $b_{ij} = c_i W_i k_{ij}$ and $D_i = c_i T_i$, for some constant c_i. Hence the coefficients satisfy the following equalities:

$$\frac{b_{11}}{k_{11}} = \frac{b_{12}}{k_{12}} \quad \text{and} \quad \frac{b_{21}}{k_{21}} = \frac{b_{22}}{k_{22}}. \tag{4.1}$$

This is the reason why it was relatively easy for Case and Casten [1] to get their result on global stability, and it is also the reason why they did not find any cases in which the outcome depends on the initial numbers of the competing predators. In fact the assumptions of Theorem 3.9(iii) give an example which violates the equalities in (4.1). This is the case which generates the unstable equilibrium in which competitive outcomes are

determined by initial numbers of predators and prey. There seem to be no compelling biological reason to assume (4.1). Therefore, there is a real possibility of situations in which the initial conditions play a role in the outcome of competition. Only in the very special case of the equality in (4.1) is it safe to assume that when the predator isoclines cross, the two-predator equilibrium is stable. This analysis should serve as a cautionary note that when one is interpreting discussions of species packing and the number of species that can coexist on a set of resources, one should not rely solely on a graphical analysis of crossing predator isoclines.

As mentioned earlier, our results can be compared with those obtained from the classical model of two-species competition introduced by Volterra [11]. MacArthur, by rearrangement of (2.1), obtained the competition coefficients (α's) and carrying capacities (K's) of classical theory from his "two-consumer, two-resource" model. If we use the notation of the present paper, MacArthur's method for computing α and K is as follows. Set $(r_j/K_j)(K_j - R_j) - k_{1j}x_1 - k_{2j}x_2 = 0$ and solve for R_j. Then substitute R_1 and R_2 into $b_{i1}R_1 + b_{i2}R_2 = D_i$. Then we have $K_1^* - x_1 - \alpha x_2 = 0$ and $K_2^* - x_2 - \alpha'x_2 = 0$, where K_1^* and K_2^* are the computed carrying capacities of predators x_1 and x_2, respectively, and α and α' are the competition coefficients of x_2 on x_1 and x_1 on x_2, respectively. In terms of present notation, these parameters are

$$K_1^* = \frac{b_{11}K_1 + b_{12}K_2 - D_1}{\frac{K_1}{r_1}b_{11}k_{11} + \frac{K_2}{r_2}b_{12}k_{12}}, \qquad K_2^* = \frac{b_{21}K_1 + b_{22}K_2 - D_2}{\frac{K_1}{r_1}o_{21}k_{21} + \frac{K_2}{r_2}b_{22}k_{22}},$$

$$\alpha = \frac{\frac{K_1}{r_1}b_{11}k_{21} + \frac{K_2}{r_2}b_{12}k_{22}}{\frac{K_1}{r_1}b_{11}k_{11} + \frac{K_2}{r_2}b_{12}k_{12}}, \qquad \alpha' = \frac{\frac{K_1}{r_1}b_{21}k_{11} + \frac{K_2}{r_2}b_{22}k_{12}}{\frac{K_1}{r_1}b_{21}k_{21} + \frac{K_2}{r_2}b_{22}k_{22}}.$$

Under the assumptions (H1), (H3), and (H4), it is easy to show that

$$\alpha' > \frac{k_2^*}{K_1^*} \quad \text{iff} \quad \frac{k_{11}}{r_1(1 - R_{1c}^*/K_1)} < \frac{k_{12}}{r_2(1 - R_{2c}^*/K_2)},$$

and

$$\alpha \frac{K_1^*}{K_2^*} \quad \text{iff} \quad \frac{k_{21}}{r_1(1 - R_{1c}^*/K_1)} < \frac{k_{22}}{r_2(1 - R_{2c}^*/K_2)}.$$

These inequalities correspond to the outcome in which there is a unique equilibrium (x_1^*, x_2^*) in the interior of the first quadrant which is a saddle point, while $(K_1^*, 0)$ and $(0, K_2^*)$ are asymptotically stable. This is the case in

which the outcome depends on the initial values. The other outcomes of classical competition theory also follow. Thus, if $\alpha' > K_2^* / K_1^*$ and $\alpha < K_1^* / K_2^*$, then the solution tends to $(K_1^*, 0)$. If $\alpha' < K_2^* / K_1^*$ and $\alpha > K_1^* / K_2^*$, then the solution tends to $(0, K_2^*)$. Finally, if $\alpha' < K_2^* / K_1^*$ and $\alpha < K_1^* / K_2^*$, then (x_1^*, x_2^*) exist and are globally asymptotically stable. It should be noted, however, that these parametric relationships assume (H1), (H3), and (H4), and are not valid in general otherwise. MacArthur apparently did not test his computed α's and K's against the competition criteria. Such a test would have shown that the Lotka-Volterra case in which the outcome depends on initial conditions could never happen in his special case (1). Moreover, by assuming (H1), (H3), and (H4), Cases I and II could not have been anticipated, nor could the great wealth of outcomes under Case III have been expected.

5. APPENDIX

Proof of Lemma 3.2. It is equivalent to show that if $b_{i1}K_1 + b_{i2}K_2 < D_i$, then $\lim_{t \to \infty} x_i(t) = 0$. Let

$$0 < \varepsilon < \frac{D_i - b_{i1}K_1 - b_{i2}K_2}{b_{i1} + b_{i2}}.$$

By Lemma 3.1 there exists $t_0 > 0$ such that $R_i(t) < K_i + \varepsilon$ for $t > t_0$, $i = 1, 2$. Then for an appropriate constant C, it follows that

$$x_i(t) = x_{i0} \exp\left(\int_0^t [b_{i1}R_1(t) + b_{i2}R_2(t) - D_i] dt \right)$$

$$< cx_{i0} \exp\{ [b_{i1}(K_1 + \varepsilon) + b_{i2}(K_2 + \varepsilon) - D_i](t - t_0) \}.$$

The first factor in the exponent is negative, so $\lim_{t \to \infty} x_i(t) = 0$.

Before beginning the proof of Theorem 3.3(ii), we note the following definitions and LaSalle's theorem [6], which will be used later.

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 and $\bar{G}$ is the closure of G. Let V be a C^1 function on R^n to R.

DEFINITION 5.1

We say V is a Liapunov function in G for (I) if $\dot{V} = \operatorname{grad} V \cdot f < 0$ on G.

THEOREM

If V is a Liapunov function G for (I), then each bounded solution $x(t)$ of (I) approaches the largest invariant set M in $E = \{ x : V(x) = 0, x \in \bar{G} \}$.

Proof of Theorem 3.3(ii), (iii), (iv). First we prove (ii). From assumptions and Lemma 3.2 it follows that $\lim_{t\to\infty} x_2(t)=0$. Let

$$0<\varepsilon<\frac{D_2-b_{21}K_1-b_{22}K_2}{b_{21}+b_{22}}, \quad \beta=\frac{k_{11}}{k_{12}}, \quad \alpha=\beta\frac{b_{12}}{k_{12}}, \quad \delta=1.$$

By Lemma 3.1 there exists $t_0>0$ such that $R_i(t)<K_i+\varepsilon$, $i=1,2,$ and

$$b_{21}K_1+b_{22}K_1+\varepsilon(b_{21}+b_{22})-D_2+\frac{k_{21}^2}{r_1/K_1}x_2(t)<0 \quad \text{for} \quad t>t_0.$$

We take as a Liapunov function V for (2.1)

$$V=R_1-\bar{R}_1-\bar{R}_1\ln\frac{R_1}{\bar{R}_1}+\alpha R_2+\beta\left(x_1-\bar{x}_1-\bar{x}_1\ln\frac{x_1}{x_1}\right)$$
$$+\delta x_2 \tag{5.1}$$

on the open set

$$Q=\{(R_1,R_2,x_1,x_2): 0<R_i<K_i+\varepsilon, \ x_i>0, \ i=1,2, \ \text{and}$$
$$b_{21}K_1+b_{22}K_2+\varepsilon(b_{21}+b_{22})-D_2+\frac{k_{21}^2}{r_1/K_1}x_2<0\}.$$

It follows that

$$\dot{V}=-\frac{r_1}{K_1}\left[(R_1-\bar{R}_1)+\frac{k_{21}}{2(r_1/K_1)}x_2\right]^2$$
$$+\alpha R_2\left[(r_2-k_{12}\bar{x}_1)-\frac{r_2}{K_2}R_2-k_{22}x_2\right]$$
$$+x_2\left[b_{21}R_1+b_{22}R_2-D_2+\frac{(k_{21})^2}{4(r_1/K_1)}x_2\right]$$
$$<\frac{r_1}{K_1}\left[(R_1-\bar{R}_1)+\frac{k_{21}}{2(r_1/K_1)}x_2\right]^2$$
$$+\alpha R_2\left[(r_2-k_{12}\bar{x}_1)-\frac{r_2}{K_2}R_2-k_{22}x_2\right]$$
$$+x_2\left[b_{21}K_1+b_{22}K_2-D_2+(b_{21}+b_{22})+\frac{k_{21}^2}{4(r_1/K_1)}\right]x_1<0 \quad \text{on } Q.$$

Hence Theorem 3.3(ii) follows directly from Lemma 3.1 and LaSalle's theorem. The proof for Theorem 3.3(iii), (iv) respectively is similar to that of

Theorem 3.3(i) except that the Liapunov functions

$$V = R_1 + \alpha\left[R_2 - \tilde{R}_2 - \tilde{R}_2 \ln\frac{R_2}{\tilde{R}_2} \right] + \beta\left[x_1 - \tilde{x}_1 - \tilde{x}_1 \ln\frac{x_1}{\tilde{x}_1} \right] + \delta x_2, \quad (5.2)$$

$$V = R_1 - R_{11}^* - \ln\frac{R_1}{R_{11}^*} + \alpha\left[R_2 - R_{12}^* - R_{12}^* \ln\frac{R_{12}}{R_{12}^*} \right]$$

$$+ \beta\left[x_1 - x_1^* - x_1^* \ln\frac{x_1}{x_1^*} \right] + \delta x_2 \qquad (5.3)$$

are used for (iii), (iv) respectively.

Proof of Theorem 3.4. From (H2) we choose $\varepsilon > 0$ such that

$$\left(\frac{D_1}{D_1} b_{21} - b_{11} \right) + b_{21}\varepsilon < 0 \quad \text{and} \quad \left(\frac{D_1}{D_2} b_{22} - b_{12} \right) + b_{22}\varepsilon < 0.$$

Let $\xi = D_1/D_2 + \varepsilon$. From (2.1) it follows that

$$\xi\frac{x_2'(t)}{x_2(t)} - \frac{x_1'(t)}{x_1(t)} = \left\{ \left(\frac{D_1}{D_2} b_{21} - b_{11} \right) + b_{21}\varepsilon \right\} R_1(t)$$

$$+ \left\{ \left(\frac{D_1}{D_2} b_{22} - b_{12} \right) + b_{22}\varepsilon \right\} R_2(t) - \varepsilon D_2$$

$$< -\varepsilon D_2.$$

Integrating from 0 to t and taking exponentials on both sides yields

$$\left(\frac{x_2(t)}{x_{20}} \right)^{\xi} < \left(\frac{x_1(t)}{x_{10}} \right) e^{-\varepsilon D_2 t} < M e^{-\varepsilon D_2 t}$$

for some $M > 0$. It follows that $\lim_{t \to \infty} x_2(t) = 0$. Using similar arguments to those in the proof of Theorem 3.3 yields Theorem 3.4.

Proof of Theorem 3.5. First we prove part (i). Since $R_{2c}^* > K_2$, we have $\lambda_{22} > K_2$, i.e., $D_2 > b_{22}K_2$. It is easy to show that $R_{2c}^* > K_2$ iff

$$\frac{\left(\frac{D_1}{D_2} b_{22} - b_{12} \right) K_2}{D_2 - b_{22}K_2} < \frac{b_{11} - \frac{D_1 b_{21}}{D_2}}{b_{21}}.$$

MacArthur's Model

Let

$$0 < \frac{\left(\dfrac{D_1}{D_2}b_{22} - b_{12}\right)K_2}{D_2 - b_{22}K_2} < \eta < \frac{b_{11} - \dfrac{D_1 b_{21}}{D_2}}{b_{21}}.$$

and choose $\epsilon > 0$ such that

$$\left\{\left(\left(\frac{D_1}{D_2}b_{22} + b_{12}\right) + b_{22}\eta\right)(K_2 + \epsilon) - \eta D_2 < 0.$$

By Lemma 3.1, there exists t_0 such that $R_2(t) < K_2 + \epsilon$ for $t > t_0$. Let $\xi = D_1/D_2 + \eta$. Then

$$\xi \frac{x_2'(t)}{x_2(t)} - \frac{x_1'(t)}{x_1(t)} = \left\{\left(\frac{D_1 b_{21}}{D_2} - b_{11}\right) + b_{21}\eta\right\} R_1(t)$$

$$+ \left\{\left(\frac{D_1}{D_2}b_{22} - b_{12}\right) + b_{22}\eta\right\} R_2(t) - \eta D_2$$

$$< \left\{\left(\frac{D_1}{D_2}b_{22} - b_{12}\right) + b_{22}\eta\right\}(K_2 + \epsilon) - \eta D_2$$

$$= \eta^* < 0$$

for $t > t_0$. From Lemma 3.1 it follows that $\lim_{t \to \infty} x_2(t) = 0$. Following the arguments in Theorem 3.4, we complete the proof of (i).

The proof of (ii) is similar to that of (i), and we omit it.

Proof of Lemma 3.6. Part (i) follows directly from a simple algebraic computation. From an elementary linear stability analysis about (E_c), the characteristic polynomial for the variational matrix evaluated at (E_c) is

$$f(z) = z^4 + A_1 z^3 + A_2 z^2 + A_3 z + A_4,$$

where

$$A_1 = \frac{r_1}{K_1} R_{1c}^* + \frac{r_2}{K_2} R_{2c}^* > 0,$$

$$A_2 = \frac{r_1 r_2}{K_1 K_2} R_{1c}^* R_{2c}^* + k_{11} b_{11} R_{1c}^* x_{1c}^* + k_{21} b_{21} R_{1c}^* x_{2c}^*$$

$$+ k_{12} b_{12} R_{2c}^* x_{1c}^* + k_{22} b_{22} R_{2c}^* x_{2c}^* > 0,$$

$$A_3 = R_{1c}^* R_{2c}^* \left[\frac{r_1}{K_1}(k_{12} b_{12} x_{1c}^* + k_{22} b_{22} x_{2c}^*) + \frac{r_2}{K_2}(k_{11} b_{11} x_{1c}^* + k_{21} b_{21} x_{2c}^*)\right] > 0,$$

$$A_4 = (k_{11} k_{22} - k_{12} k_{21})(b_{11} b_{22} - b_{12} b_{21}) R_{1c}^* R_{2c}^* x_{1c}^* x_{2c}^*.$$

From the Routhe-Hurwitz criterion, (E_c) is asymptotically stable if and only if $A_4 > 0$ and $A_3(A_1 A_2 - A_3) > A_1^2 A_4$. By (H3) we have $b_{11} b_{22} > b_{12} b_{21}$. Hence (ii) follows. We note that it is hard to verify $A_3(A_1 A_2 - A_3) > A_1^2 A_4$.

If $C_2 > C_1$, then $A_4 < 0$ and (E_c) is unstable. Since $A_4 < 0$, it is impossible that each root of $f(z) = 0$ has positive real part. Hence (iii) follows.

Proof of Lemma 3.7.

$$R_{11}^* < R_{1c}^* \iff b_{12}\left[\frac{r_1}{k_{11}} - \frac{r_2}{k_{12}}\left(1 - \frac{\lambda_{12}}{K_2}\right)\right] < R_{1c}^*\left(\frac{r_1}{k_{11}}\frac{b_{12}}{K_1} + \frac{r_2}{k_{12}}\frac{b_{11}}{K_2}\right)$$

$$\iff \frac{r_1}{k_{11}} b_{12}\left(1 - \frac{R_{1c}^*}{K_1}\right) < \frac{r_2}{k_{12}}\left[b_{12}\left(1 - \frac{\lambda_{12}}{K_2}\right) + \frac{b_{11}}{K_2} R_{1c}^*\right]$$

$$\iff \frac{r_1}{k_{11}}\left(1 - \frac{R_{1c}^*}{K_1}\right) < \frac{r_2}{K_{12}}\left(1 - \frac{\lambda_{12}}{K_2} + \frac{1}{K_2}\frac{b_{11}}{b_{12}} R_{1c}^*\right)$$

$$= \frac{r_2}{k_{12}}\left(1 - \frac{\lambda_{12}}{K_2} + \frac{1}{K_2}\frac{1}{b_{12}}(D_1 - b_{12} R_{2c}^*)\right)$$

$$= \frac{r_2}{k_{12}}\left(1 - \frac{R_{2c}^*}{K_2}\right)$$

$$\iff P_{12} < P_{11}.$$

Hence (i) follows. Similarly we have (ii).

Proof of Lemma 3.8. First we prove (i). Let

$$T^* = \frac{r_1\left(1 - \frac{R_{1c}^*}{K_1}\right)}{r_2\left(1 - \frac{R_{2c}^*}{K_2}\right)}, \qquad \alpha(\varepsilon) = \frac{1}{T^*} + \varepsilon \qquad \xi(\varepsilon) = \frac{\frac{r_1}{K_1} b_{12}\alpha(\varepsilon) + \frac{r_2}{K_2} b_{11}}{b_{22} b_{11} - b_{12} b_{21}},$$

$$\beta(\varepsilon) = \frac{\frac{r_1}{K_1} b_{22}\alpha(\varepsilon) + \frac{r_2}{K_2} b_{21}}{b_{22} b_{11} - b_{12} b_{21}}, \qquad \rho(\varepsilon) = r_2 - \xi(\varepsilon) D_2 - \alpha(\varepsilon) r_1 + \beta(\varepsilon) D_1,$$

where $\varepsilon > 0$ is a small parameter. Then

$$\frac{R_2'(t)}{R_2(t)} + \xi(\varepsilon)\frac{x_2'(t)}{x_2(t)} - \alpha(\varepsilon)\frac{R_1'(t)}{R_1(t)} - \beta(\varepsilon)\frac{x_1'(t)}{x_1(t)}$$

$$= \rho(\varepsilon) + [-k_{12} + \alpha(\varepsilon) k_{11}] x_1(t) + [-k_{22} + \alpha(\varepsilon) k_{21}] x_2(t). \quad (5.8)$$

It is easy to verify

$$\rho(0) = r_2 - \frac{r_1}{T^*} + \frac{1}{b_{22}b_{11} - b_{12}b_{21}} \frac{r_1}{K_1 T^*} (b_{22}D_1 - b_{12}D_2)$$

$$+ \frac{r_2}{K_2} \frac{b_{21}D_1 - b_{11}D_2}{b_{22}b_{11} - b_{12}n_{21}}$$

$$= r_2\left(1 - \frac{R_{2c}^*}{K_2}\right) - \frac{r_1}{T^*}\left(1 - \frac{R_{1c}^*}{K_1}\right) = 0$$

and

$$\frac{d\rho}{d\varepsilon} = r_1\left[\frac{R_{1c}^*}{K_1} - 1\right] < 0.$$

Since $P_{22} > P_{21}$ and $P_{12} > P_{11}$, it follows that $T^* > C_1, C_2$. We choose $\varepsilon^* > 0$ small enough that $\rho(\varepsilon^*) < 0$, $\xi(\varepsilon^*) > 0$, $-k_{12} + \alpha(\varepsilon^*)k_{11} < 0$, and $-k_{22} + \alpha(\varepsilon^*)k_{21} < 0$. Then from (5.8) and Lemma 3.1, it follows that $R_2(t)[x_2(t)]^{\xi(\varepsilon^*)} < M e^{\rho(\varepsilon^*)t}$ for some constant $M > 0$ and hence $\lim_{t\to\infty} R_2(t)[x_2(t)]^{\xi(\varepsilon^*)} = 0$. We claim $\lim_{t\to\infty} R_2(t)x_2(t) = 0$. If $\xi(\varepsilon^*) > 1$, then $[R_2(t)x_2(t)]^{\xi(\varepsilon^*)} = [R_2(t)]^{\xi(\varepsilon^*)-1}$. But $R_2(t)[x_2(t)]^{\xi(\varepsilon^*)} < (R_{2,\max})^{\xi(\varepsilon^*)-1}R_2(t)[x_2(t)]^{\xi(\varepsilon^*)} \to 0$ as $t\to\infty$. Hence $\lim_{t\to\infty} R_2(t)x_2(t) = 0$. If $\xi(\varepsilon^*) < 1$, then

$$R_2(t)x_2(t) = [x_2(t)]^{1-\xi(\varepsilon^*)} R_2(t)[x_2(t)]^{\xi(\varepsilon^*)}$$

$$> \left(\sup_{0 < t < \infty} x_2(t)\right)^{1-\xi(\varepsilon^*)} [R_2(t)x_2(t)]^{\xi(\varepsilon^*)}$$

$$\to 0 \qquad \text{as} \quad t\to\infty.$$

Hence we complete the proof of (i).

The proof of (ii) is similar to that of (i). Let $\alpha(\varepsilon) = T^* + \varepsilon$,

$$\xi(\varepsilon) = \frac{\frac{r_1}{K_1}b_{22} + \frac{r_2}{K_2}b_{21}\alpha(\varepsilon)}{b_{11}b_{22} - b_{12}b_{21}}, \qquad \beta(\varepsilon) = \frac{\frac{r_1}{K_1}b_{12} + \frac{r_2}{K_2}b_{11}\alpha(\varepsilon)}{b_{11}b_{22} - b_{12}b_{21}},$$

and $\rho(\varepsilon) = r_1 - \xi(\varepsilon)D_1 - \alpha(\varepsilon)r_2 + \beta(\varepsilon)D_2$. Then we have $\rho(0) = 0$ and $d\rho/d\varepsilon = r_2(R_{2c}^*/K_2 - 1) < 0$. Since $P_{21} > P_{22}$ and $P_{11} > P_{12}$, it follows that $T^* < C_1, C_2$. We choose $\varepsilon^* > 0$ such that $\rho(\varepsilon^*) < 0$, $\alpha(\varepsilon^*) < C_1, C_2$, $\xi(\varepsilon^*) > 0$. Then we have

$$\frac{R_1'(t)}{R_1(t)} + \xi(\varepsilon^*)\frac{x_1'(t)}{x_1(t)} - \alpha(\varepsilon^*)\frac{R_2'(t)}{R_2(t)} - \beta(\varepsilon^*)\frac{x_2'(t)}{x_2(t)}$$

$$= \rho(\varepsilon^*) + [-k_{11} + \alpha(\varepsilon^*)k_{12}]x_1(t) + [-k_{21} + \alpha(\varepsilon^*)k_{22}]x_2(t)$$

$$> \rho(\varepsilon^*) < 0.$$

Hence $\lim_{t\to\infty} R_1(t)[x_1(t)]^{E(\epsilon^*)} = 0$ and $\lim_{t\to\infty} R_1(t)x_1(t) = 0$.

Proof of Theorem 3.9(i). First we prove part (a). Since $T^* > C_1, C_2$, from Lemma 3.8 it follows that $\lim_{t\to\infty} R_2(t)x_2(t) = 0$. From assumption (A1), the equilibrium $(E_{11}) = (\bar{R}_1, 0, \bar{x}_1, 0)$ exists. Let $\beta = k_{11}/b_{11}$, $\alpha = \beta b_{12}/k_{12}$, and $\delta = k_{21}/b_{21}$. Since $b_{21}\bar{R}_1 - D_2 < 0$, we have $r_2 < k_{12}\bar{x}_1$ and $\lim_{t\to\infty} R_2(t)x_2(t) = 0$. There exists $t_0 > 0$ such that for $t > t_0$

$$\delta(b_{21}\bar{R}_1 - D_2) - \frac{(\delta b_{22} - \alpha k_{22})^2}{4\alpha(r_2 - k_{12}\bar{x}_1)} R_2(t)x_2(t) < 0.$$

Let the Liapunov function V be (5.1) with α, β, δ above, defined on open set

$$Q = \Big\{(R_1, R_2, x_1, x_2): x_i, R_i > 0, \ i = 1, 2, \text{ and}$$

$$\delta(b_{21}\bar{R}_1 - D_2) - \frac{(\delta b_{22} - \alpha k_{22})^2}{4\alpha(r_2 - k_{12}\bar{x}_1)} R_2 x_2 < 0\Big\}.$$

It follows that

$$\dot{V} = -\frac{r_1}{K_1}(R_1 - \bar{R}_1)^2 + \alpha R_2\Big[-\frac{r_2}{K_2}R_2 + (r_2 - k_{12}\bar{x}_1) - k_{22}x_2\Big]$$

$$+ \delta x_2\Big[b_{22}R_2 + (b_{21}\bar{R}_1 - D_2)\Big]$$

$$= -\frac{r_1}{K_1}(R_1 - \bar{R}_1)^2 - \alpha\frac{r_2}{K_2}R_2^2$$

$$+ \alpha(r_2 - k_{12}\bar{x}_1)R_2\Big(1 + \frac{\delta b_{22} - \alpha k_{22}}{2\alpha(r_2 - k_{12}\bar{x}_1)}x_2\Big)^2$$

$$+ x_2\Big[\delta(b_{21}\bar{R}_1 - D_2) - \frac{(\delta b_{22} - \alpha k_{22})^2}{4\alpha(r_2 - k_2\bar{x}_1)}R_2 x_2\Big]$$

$$< 0 \quad \text{on } Q.$$

Then Theorem 3.9(i) (a) follows from Lemma 3.1 and LaSalle's theorem.

Let (A3) hold. Theorem 3.9(i) (b) follows directly from Lemmas 3.7, 3.8.

Proof of Theorem 3.9(iii). Theorem 3.9(iii) follows directly from Lemma 3.6, Lemma 3.7.

Proof of Theorem 3.9(iv). From Lemma 3.6, it follows that (E_c) exists. By Remark 2, we have four cases, namely, (A2)(B1), (A3)(B1), (A2)(B3), (A3)(B3). We just show one case; the rest of them follow in the same way. Let (A2)(B1) hold. If $\lim_{t\to\infty} x_2(t) = 0$, then using the arguments in the proof of part (ii) of Theorem 3.4 yields $\lim_{t\to\infty} R_1(t) = 0$, $\lim_{t\to\infty} R_2(t) = \lambda_{12} = \bar{R}_2$,

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$\lim_{t \to \infty} x_1(t) = \bar{x}_1$. From (2.1), $x_2(t)$ becomes unbounded as $t \to \infty$. This is the desired contradiction. Hence $\limsup_{t \to \infty} x_2(t) > 0$.

Similarly, if $\lim_{t \to \infty} x_1(t) = 0$, then $\lim_{t \to \infty} R_1(t) = \lambda_{21}$, $\lim_{t \to \infty} R_2(t) = 0$, and $x_1(t)$ becomes unbounded. Hence $\limsup_{t \to \infty} x_1(t) > 0$.

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