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A CONTRIBUTION TO THE THEORY OF COMPETING PREDATORS[1]

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Abstract. This paper concerns the growth of 2 predator species competing exploitatively for the same prey population. The prey population grows logistically in the absence of predation, and the predators 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 of which predator species will survive and which will not, given the growth parameters of the prey and the functional response parameters of the 2 predators. Which predator wins or loses depends critically on the relative magnitude of the prey carrying capacity, K, and the λ parameters of the 2 predators. λ_i represents the prey density at which the ith predator "breaks even" (equal birth and death rates). This prey density is defined by the product of the predator's half-saturation (Michaelis-Menten) constant times the ratio of the predator's death rate to its intrinsic rate of increase. Coexistence is also possible for a wide range of parameters, but only as a periodic solution. A primary conclusion is that coexistence is possible only if the predator with the smaller half-saturation constant also has the smaller birth-rate-to-death-rate ratio. This necessary constraint is the mechanistic equivalent to requiring that 1 predator be an "r-strategist" and the other be a "K-strategist." This condition is insufficient to guarantee coexistence, however. If the prey carrying capacity, K, is "too small" the K-strategist wins, and if K is "too large," the r-strategist wins. The bounded region of intermediate K values permitting coexistence is defined by the functional response parameters of the 2 predator species. The greater the disparity between the half-saturation constants of the 2 predators, the larger the region of K permitting coexistence.

Key words: coexistence; competition; exclusion; mathematical model; predation.

INTRODUCTION

Although competition between species exploiting a common prey population is probably of frequent occurrence in nature, little theoretical work has been done on such systems. Models have usually considered the competitors without explicit concern for the dynamics of the prey population, or else the question of competition is dropped entirely to consider only the dynamics of a 1 predator–1 prey system. This paper and a companion paper (Hsu et al. 1978) discusses a model of 2 predators competing exploitatively for a common prey species, in which the dynamics of all 3 species are specifically included.

MacArthur (1972) was 1 of the first to consider prey dynamics in models of competition. He considered a system of equations in which logistic growth characterizes the resource or resources in the absence of the consumer species. For 1 resource and 2 consumers, these equations are:

$$\frac{1}{R}\frac{dR}{dt} = r\left[1 - \frac{R}{K}\right] - a_1X_1 - a_2X_2,$$

$$\frac{1}{X_1}\frac{dX_1}{dt} = C_1[a_1w_1R - T_1],$$

$$\frac{1}{X_2}\frac{dX_2}{dt} = C_2[a_2w_2R - T_2],$$

where R is the quantity of resource or prey, and X_1 and X_2 are the quantities of the 2 predator species. The parameters of this system are:

r = intrinsic rate of increase of prey,
K = carrying capacity for prey population,
a_1, a_2 = rate of capture of prey, expressed per individual prey and predator, for species X_1 and X_2, respectively,
w_1, w_2 = yield of predator weight produced per unit prey consumed per individual predator, for species X_1 and X_2.

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C_1, C_2 = conversion factor for weight to new predator individuals, and
T_1, T_2 = weight of food needed to just maintain predator populations without growth.

While these equations allow for logistic growth in the prey population, they also make the assumption that the functional response of individual predators to prey density is linear. The linear assumption is useful because it simplifies analysis when >1 resource is present. However, there are now extensive laboratory and field studies of the feeding behavior of individual predators (Tinbergen 1960; Ivlev 1961; Holling 1965, 1966; Royama 1971; Hassell 1978, and others) which demonstrate that feeding rate does not increase linearly with prey abundance. Rather, feeding rates saturate at limits set by the time required for "handling" prey items and for digestion.

May (1972), Gilpin (1972), and Shimazu et al. (1972) incorporated a saturating functional response into an equation system for a single prey and single predator, and independently discovered that limit cycles occurred in the asymptotic behavior under certain conditions. This contrasts with the behavior of the classical Nicholson-Bailey model, which has unrestrained exponential growth of the prey in the absence of the predator and a linear predator functional response. The Nicholson-Bailey model exhibits cycles of neutral stability around a critical point which is a "center." These cycles have amplitudes which are determined entirely by initial conditions, a very unrealistic feature. Gilpin (1972) found limit cycles by numerical experiments on a computer, and Shimazu et al. (1972) also found limit cycles by simulation after showing by local linearized analysis that the nonzero critical point was unstable for some parameter values.

May (1972) treated a large class of predator–prey models with a variety of functions for saturating feeding rates and self-limited prey populations in relation to Kolmogorov's (1936) theorem. He showed that when predator and prey persist, either a stable equilibrium occurs between predator and prey, or else the critical point is unstable and is surrounded by a limit cycle. Recently, however, Albrecht et al. (1973) and Albrecht et al. (1974) have demonstrated that May's (1972) conclusion was not precisely correct. It is only possible to assert that either (1) a stable limit cycle exists, or (2) a pair of semi-stable orbits exist, 1 inside the other. In this case, the innermost orbit is approached asymptotically from any point inside it (except the critical point), and the outer orbit is approached from any point in the first quadrant outside the outer orbit. Points in between the semi-stable orbits may be in neutrally stable orbits whose paths are determined by initial conditions.

Recently, Koch (1974) studied the numerical behavior of a system of equations identical to the system discussed in this paper, and discovered the remarkable fact that coexistence was possible between 2 predators competing for the same regenerating resource. Coexistence was possible for a broad region of parameters, and was achieved as a periodic solution, not a constant equilibrium. McGehee and Armstrong (1977) show that, in general, it is possible to get more than n species coexisting on n resources if the assumption of linearity of predator functional response to prey density is relaxed. We add a further requirement: coexistence is generally not possible if the resource is regenerated at a constant rate and the competing predators are continually consuming the resource (Hsu et al. 1977), whether or not the predators have a nonlinear functional response. The 1 exception is the special case of coexistence which arises if and only if the λ parameters (see below) are identical for both species.

The existence in nature of stable limit cycles in simple predator–prey systems seems a real possibility. We demonstrate below that permanent oscillations arise for a wide range of biological parameter values that almost certainly occur in nature. It seems unlikely that the well-known cases of natural cycling are due to neutrally stable oscillations, as would be required by the Nicholson-Bailey model. If neutral stability were the case, we might expect much more variance from habitat to habitat in cycle amplitude for a given predator–prey system than is actually observed, because the amplitude would be determined by the sizes of the original founding populations and by subsequent buffeting by stochastic forces. On a cautionary note, however, it may be difficult in practice to distinguish a limit cycle from the behavior of a damped oscillatory system which is continually perturbed away from equilibrium.

To our knowledge, there have been no specific attempts to prove whether oscillations of predator and prey in the field are limit cycles. Lidicker (1973) studied the population dynamics of *Microtus californicus* for 13 yr after its introduction onto tiny Brooks Island in San Francisco Bay. On the mainland where there are many predators, the vole cycled with dramatic regularity every 3 or 4 yr, and the peaks and lows were reasonably reproducible numerically. On the island, where there was no predation (except for occasional acts of cannibalism), the population had a less-pronounced cycle with annual peaks, and peaks every 2nd yr that were a little higher. Whether the cycles on the mainland are caused by predators is in some dispute, but Pearson (1966) demonstrated that vole-killing by feral cats in the East Bay area did accentuate the cycle by deepening the lows. The major crash in numbers may be due to an interaction of the voles with their grassland food supplies (Batzli and Pitelka 1971, 1975). Whether the cycling occurs because of predators killing voles, or voles eating their plant food supplies, or some combination of the 2, the fact remains that both predators on the voles and the voles themselves exhibit saturating functional responses to the density of

their food resources. Moreover, the food resources themselves have powers of regeneration, and these powers are limited by density-dependent factors. These facts create the conditions necessary for the expression of limit cycles.

The saturating predator functional response used in the present analysis is that proposed by Holling (1965) for "nonlearning" predators. The label nonlearning is a bit misleading because even predators capable of learning should exhibit this type of response when given only 1 type of prey for which to search. The derivation of this response is as follows: Holling (1965) observed that there were 2 basic time-consuming elements of the "attack cycle" for a predator: (1) search time and (2) handling time (including digestion). If we let T equal the total attack cycle time, T_s equal the search time, h equal the handling time per prey item and N_a equal the number of prey items caught during the attack cycle, then

$$T = T_s + h \cdot N_a. \tag{1.1}$$

Holling (1965) then showed that the number of prey items caught is proportional to the density of prey (S) and to the search time, T_s:

$$N_a = c \cdot S \cdot T_s \tag{1.2}$$

where c is the encounter rate per unit prey density. In the Nicholson-Bailey model, the slope of the feeding rate curve with prey density is constant with slope c. However, this is not the case here: as prey density increases, the slope of the functional response (feeding rate) decreases. Eliminating T_s between Eqs. 1.1 and 1.2 and rearranging gives an expression for the number attacked.

$$N_a = \frac{c \cdot S_2 \cdot T}{1 + c \cdot h \cdot S}.$$

Then the number caught per unit time, F, is the feeding rate, and is given by:

$$F = \frac{N_a}{T} = \frac{c \cdot S}{1 + c \cdot h \cdot S}. \tag{1.3}$$

This is the feeding rate per individual predator. The total consumption by the predator population as a whole is given by $F \cdot X$, where X is the number of predators in the population. The maximum feeding rate is given by the inverse of handling time, $1/h$; this rate is achieved as S, the density of prey, becomes large.

Saturating functional responses of this kind are nearly universal in biological rate processes. At the level of enzyme-mediated reactions, Eq. 1.3 is the well-known Michaelis-Menten equation, which is usually written:

$$v = \frac{V_m \cdot S}{K_m + S}, \tag{1.4}$$

where v is the specific rate of product formation or nutrient uptake, V_m is the maximum specific rate of product formation or nutrient uptake, S is resource density or substrate concentration, and K_m (the half-saturation constant) is the substrate concentration at which the rate of product formation or nutrient uptake is half maximal. Equation 1.4 has 2 constants which are easily converted from the constants in Holling's (1965) functional response, Eq. 1.3: $K_m = 1/ch$ and $V_m = 1/h$ The relationship between the Holling (1965) functional response and Michaelis-Menten kinetics has been explored in more detail by Real (1977).

In summary, the most important biological features of Eqs. 1.3 and 1.4 are: (a) at low resource density, the rate of uptake is limited by, and proportional to, resource concentration, whereas (b) at high resource density, the rate is limited by processing time (enzyme-substrate complex turnover time in enzyme-mediated reactions; handling time in predator–prey interactions), and is independent of resource concentration. In this paper, we have chosen to use the Michaelis-Menten formulation because the representation of the function is a little simpler in Eq. 1.4 than in 1.3.

Statement of the Model

This paper concerns the behavior of a predator–prey system consisting of 2 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. Both species have access to prey and compete only by lowering the population of shared prey. Death rates are assumed to be such 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 the functional responses of the predators obey the Holling (1965) "disc" (nonlearning) curve. With these assumptions, the model is given by:

$$\begin{aligned}
\frac{dS(t)}{dt} &= \gamma S(t)[1 - S(t)/K] - \left(\frac{m_1}{y_1}\right)\left(\frac{x_1(t)S(t)}{a_1 + S(t)}\right) \\
&\quad - \left(\frac{m_2}{y_2}\right)\left(\frac{x_2(t)S(t)}{a_2 + S(t)}\right), \\
\frac{dx_1(t)}{dt} &= \frac{m_1 x_1(t)S(t)}{a_1 + S(t)} - d_1 x_1(t), \\
\frac{dx_2(t)}{dt} &= \frac{m_2 x_2(t)S(t)}{a_2 + S(t)} - d_2 x_2(t),
\end{aligned} \tag{1}$$

where S, x_1, and x_2 are all positive at $t = 0$. The symbols are as follows: $x_i(t)$ is the number of the ith 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 ith predator, d_i is the death rate for the ith predator, y_i is the yield conversion factor for the ith predator feeding on the prey, a_i is the half-saturation constant for the ith 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 questions: Under what conditions will neither, 1, or both species of predator survive or die out? Secondly, if 1 or both predators survive, what is their steady-state or limiting behavior in terms of population numbers?

Summary of Analytical Results

In the companion paper (Hsu et al. 1978), we give formal proofs for the following results, which are summarized here for later reference.

We noted first that the system is "well-behaved" mathematically in the sense that the model will never produce negative values of S, x_1, or x_2, provided that the initial values of S, x_1, and x_2 are nonnegative. This is an essential first requirement of any realistic ecological model.

Secondly, we established that there is a minimum prey population size that can support a given predator, even in the absence of competition. For the ith predator, let $\lambda_i = a_i(d_i/r_i)$, where $r_i = m_i - d_i$, the predator's intrinsic rate of increase. The predator cannot survive on the prey if $\lambda_i \geq K$, the prey carrying capacity. This result is independent of any competition from rival predators. We also noted that the predator will die out if $m_i \leq d_i$. Obviously, if the predator's maximal birth rate is less than or equal to its death rate, no amount of prey will sustain the predator. Hence, as one would expect, if $\lambda \geq K$ and/or if $m \leq d$ for both predators, x_1 and x_2 die out and S approaches K.

The parameter λ_i is important for the rest of the analysis as well because its relative value for the 2 competing predators plays a role in determining which species will survive and which will not. Note that λ_i has units of prey density (the units of the half-saturation constant, a_i) because the units of d_i and r_i cancel. Another parameter, $b_i = m_i/d_i$, the ratio of the ith predator's maximal birth and death rates, will also be important.

Next, we showed that if predator species 2 cannot be supported by the prey population even in the absence of competition, but predator 1 can, and if K is small enough, then the predator–prey system will approach the asymptotically stable equilibrium point $(S^*, x^*_1, 0)$. This happens when $(K - a_1)/2 < \lambda_1 < K$ for predator 1, and either $r_2 \leq 0$ or $K \leq \lambda_2$ for predator 2. At equilibrium, $S^* = \lambda_1$ and

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

If K is larger, such that $\lambda_1 < (K - a_1)/2$ (but such that K is still less than λ_2, or else $r_2 \leq 0$), then predator 2 dies out and the prey and predator 1 enter permanent oscillations. Although these 2 results were known previously for the 1-predator case by numerical analysis and local stability analysis of the critical points, our extension to 2 predators is new; and our analysis is "global."

Of more interest biologically is what happens when the carrying capacity of the prey is adequate to support either predator in the absence of competition, i.e., when $0 < \lambda_1 < \lambda_2 < K$. This case was partially resolved by analytical means, and we have completed the study of this case numerically in this paper. When $\lambda_1 < \lambda_2 < K$, (1) if $a_1 \geq a_2$, or (2) if $a_1 < a_2$ but $b_1 \geq b_2$, then predator 1 will win and predator 2 will die out. The surviving predator and the prey approach an equilibrium point or a periodic solution, depending on whether $\lambda_1 >$ or $< (K - a_1)/2$, respectively. Note that in case (1) the surviving predator wins in spite of the disadvantage of having a larger half-saturation constant than its rival. The surviving predator wins because of its smaller λ, even though it needs a higher prey density to reach its half-maximal birth rate than does its losing rival.

It should be noted that predator 2 wins and predator 1 dies out when the subscripts are reversed in the above cases.

The only case left is when $a_1 < a_2$ and $b_1 < b_2$. This corresponds to the biological situation in which the predator with the smaller half-saturation constant also has the smaller birth rate/death rate ratio. In this region of parameter space, we have 1 useful analytical result for small K. When $a_1 < a_2$ and $b_1 < b_2$, and

$$K < \frac{a_2b_1 - a_1b_2}{b_2 - b_1},$$

then predator 1 wins and predator 2 dies out. Note that these conditions imply that $\lambda_1 < \lambda_2 < (a_2b_1 - a_1b_2)/(b_2 - b_1)$. For K above this value, we must turn to numerical analysis.

Numerical Results

From the numerical studies reported below, we know that the predators can coexist in a portion of the parameter space defined by $\lambda_1 < \lambda_2$, $a_1 < a_2$, $b_1 < b_2$, and $K > (a_2b_1 - a_1b_2)/(b_2 - b_1)$. Therefore, necessary conditions which must be satisfied for coexistence of the predators on the shared prey species are that

$$\frac{r_1}{r_2} < \frac{d_1}{d_2} < \frac{a_2r_1}{a_1r_2}$$

and

$$K > \frac{a_2b_1 - a_1b_2}{b_2 - b_1}$$

Note that these criteria do not necessarily require that the predator having the lower half-saturation constant also has a lower intrinsic rate of increase; but it

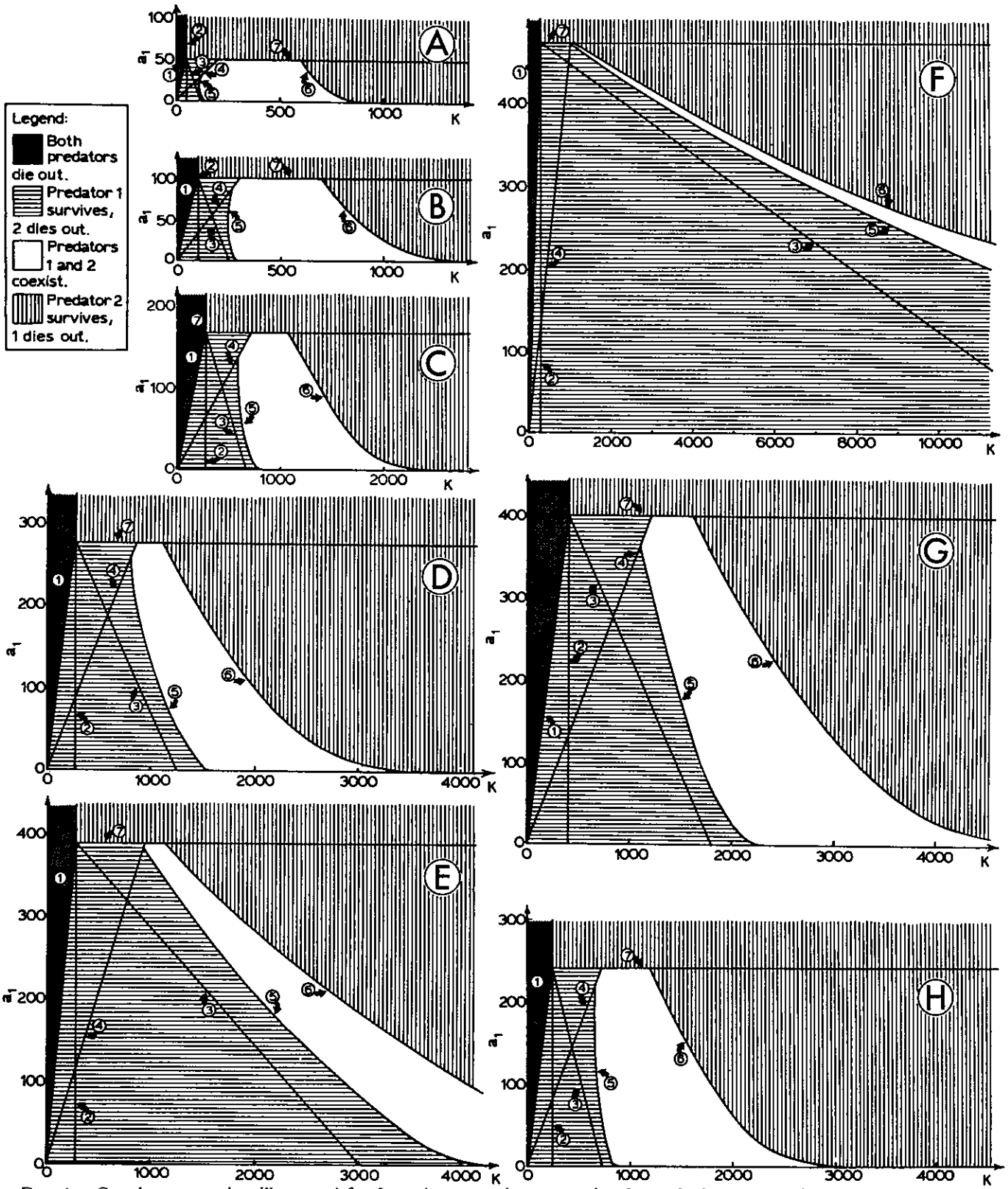

FIG. 1. Coexistence region illustrated for 2 predator species competing for a single prey species. Parameter space is a plot of prey carrying capacity, K, on the x-axis against the half-saturation constant for predator 1, a_1, on the y-axis. Parameters fixed for all graphs: prey intrinsic rate of increase, $\gamma = 20 \cdot \ln 2$; death rate of predator 1, $d_1 = \ln 2/2$; death rate of predator 2, $d_2 = \ln 2$; yield constant for predator 1, $y_1 = 0.1$; yield constant for predator 2, $y_2 = 1.4$. Parameters varied: the half-saturation constant for predator 2, a_2, and the maximum birth rates of predators 1 and 2, m_1 and m_2, respectively. The parameter, b_i, is the ratio of m_i to d_i for the ith predator. The parameter values for each case: (A) $a_2 = 500$, $m_1 = \ln 2$ ($b_1 = 2$), $m_2 = 11 \cdot \ln 2$ ($b_2 = 11$); (B) $a_2 = 500$, $m_1 = \ln 2$ ($b_1 = 2$), $m_2 = 6 \cdot \ln 2$ ($b_2 = 6$); (C) $a_2 = 500$, $m_1 = 0.8 \cdot \ln 2$ ($b_1 = 1.6$), $m_2 = 2.8 \cdot \ln 2$ ($b_2 = 2.8$); (D) $a_2 = 500$, $m_1 = \ln 2$ ($b_1 = 2$), $m_2 = 2.8 \cdot \ln 2$ ($b_2 = 2.8$); (E) $a_2 = 500$, $m_1 = 1.2 \cdot \ln 2$ ($b_1 = 2.4$); $m_2 = 2.8 \cdot \ln 2$ ($b_2 = 2.8$); (F) $a_2 = 500$, $m_1 = 1.35 \cdot \ln 2$ ($b_2 = 2.7$), $m_2 = 2.8 \cdot \ln 2$ ($b_2 = 2.8$); (G) $a_2 = 720$, $m_1 = \ln 2$ ($b_1 = 2$), $m_2 = 2.8 \cdot \ln 2$ ($b_2 = 2.8$); (H) $a_2 = 720$, $m_1 = \ln 2$ ($b_1 = 2$), $m_2 = 4 \cdot \ln 2$ ($b_2 = 4$). Numbered lines are as follows: (1): $\lambda_1 = K$; (2): $\lambda_2 = K$; (3): $K = (a_2 b_1 - a_1 b_2)/(b_2 - b_1)$; (4): $\lambda_1 = (K - a_1)/2$; (5): Lower $K - a_1$ boundary for coexistence region (known from numerical analysis); (6): Upper $K - a_1$ boundary for coexistence region (known from numerical analysis); (7): $\lambda_1 = \lambda_2$. See text for explanation of variables.

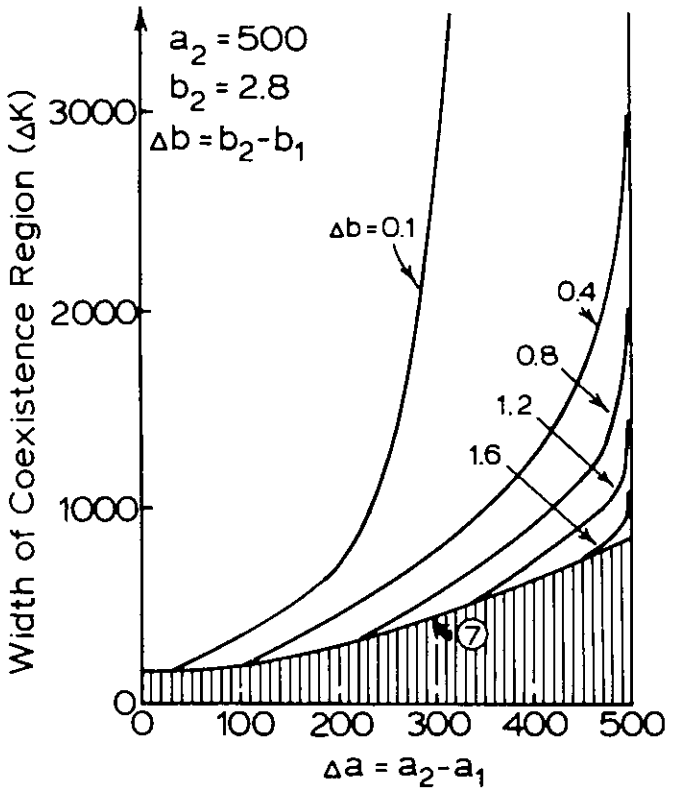

FIG. 2. Width of coexistence region, measured in terms of range of prey carrying capacities, K, as a function of the magnitude of the difference between the half-saturation constants of the 2 predators, Δa, and of the difference between the birth rate/death rate ratios of the 2 predators, Δb. Other parameters as in Fig. 1.

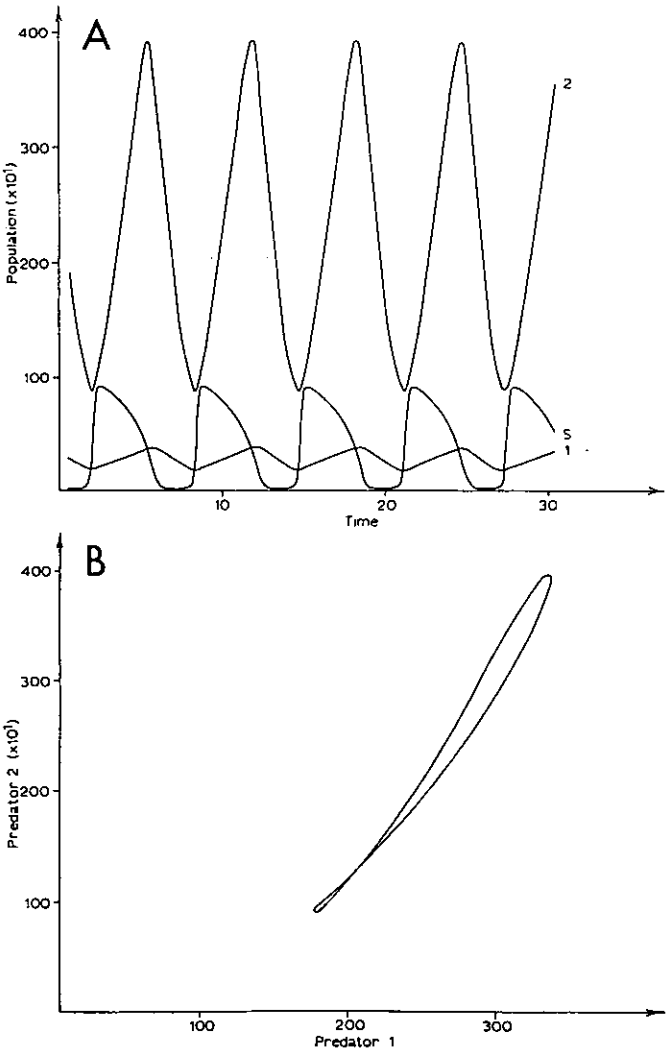

FIG. 3. Case in which there is oscillatory coexistence of 2 predator species (1 and 2) on a single prey species, S. Parameters are the same as in Fig. 1D with the half-saturation constant of predator 1, $a_1 = 200$ and the prey carrying capacity, $K = 1100$. (A) Oscillations as a function of time. (B) Limit cycle of numbers of predator 1 plotted against numbers of predator 2. Initial values: Number of predator 1, $x_1 = 307.13$, number of predator 2, $x_2 = 2684.95$, number of prey, $S = 8.60$.

does require this predator to have a lower ratio of birth rate to death rate (lower b_i), which is equivalent to $r_1/d_1 < r_2/d_2$.

Whether 1 predator wins or loses in this region, or whether the predators coexist, depends critically upon the magnitude of the prey carrying capacity, K. When K is small, the predator with the smaller half-saturation constant and birth rate/death rate ratio wins; and when K is large, the predator with the larger half-saturation constant and birth rate/death rate ratio wins. In between, there is always a nonzero interval of intermediate K values for which both predators coexist. The coexistence region can be made indefinitely large by appropriate choice of parameters. The region is independent of γ, the intrinsic rate of increase of the prey population.

The region of coexistence is clearly revealed if we make a plot of predator 1's half-saturation constant, a_1, on the y-axis against the prey carrying capacity, K, on the x-axis (Figs. 1A–1H). The portion of the $K - a_1$ plane of interest is the region $0 < a_1 < a_2$ and $0 < K < \infty$. Also, a second inequality must be satisfied for there to be any possibility of coexistence: $b_1 < b_2$. All other parameters except K and a_1 are held constant in each figure. The series of numbered lines indicate all boundaries between competitive outcomes. The straight lines are boundaries known from analysis, whereas the 2 curves are boundaries determined by simulation. The boundaries are numbered in an equivalent way in each figure.

Lines 1 and 2 mark the lower limits on prey K for respective predators 1 and 2 to survive even in the absence of competition; K values to the left of both lines will result in both predators dying out. Line 3 is the criterion $K = (a_2b_1 - a_1b_2)/(b_2 - b_1)$. Values of K smaller than this result in predator 2 losing to predator 1, provided $\lambda_1 < \lambda_2$ (line 7) and $\lambda_1 < K$ (line 1). Line 4 is the boundary given by $K = a_1 + 2\lambda_1$; values of K smaller than this again result in predator 1 winning, also provided, however, that $\lambda_1 < \lambda_2$ and $\lambda_1 < K$. For $K <$ line 4, predator 1 approaches a constant number, and for $K >$ line 4, predator 1, if it survives, is permanently oscillatory in numbers. Curves 5 and 6 mark the boundaries of the parameter region in which pred-

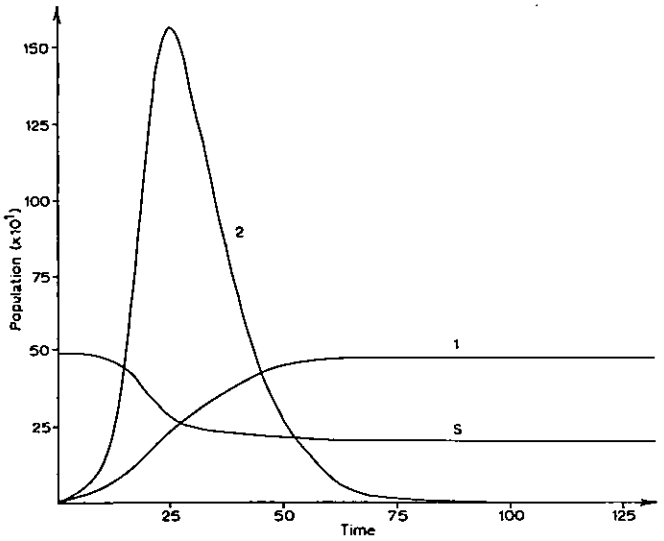

FIG. 4. Case in which predator 2 ("r-strategist") dies out, and predator 1 ("K-strategist") and the prey approach a constant equilibrium. Parameters are the same as in Fig. 1D with half-saturation constant for predator 1, $a_1 = 200$ and the prey carrying capacity, $K = 500$. Initial values: number of predator 1, $x_1 = 10$, $x_2 = 10$, number of prey, $S = 480$.

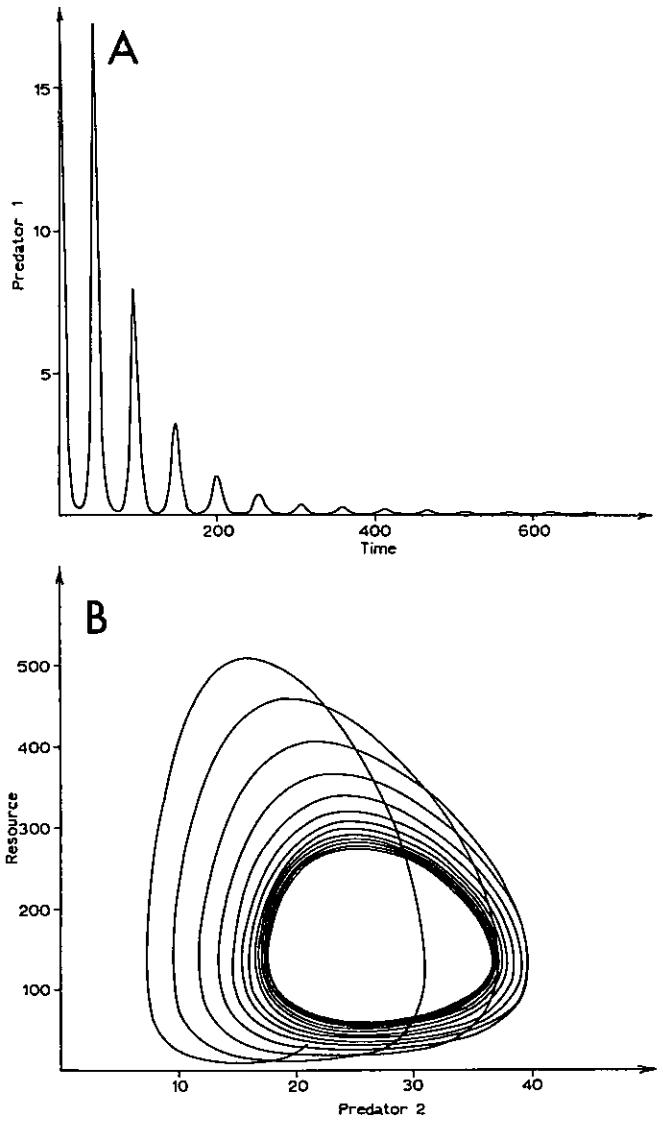

FIG. 5. Case in which predator 1 ("K = strategist") dies out, and predator 2 ("r-strategist") and the prey approach a limiting periodic solution. (A) Oscillations of predator 1 as it dies out; (B) Approach of predator 2 and prey (here labelled "resource") to a limiting periodic solution. Parameters are the same as in Fig. 4 except prey intrinsic rate of increase, $\gamma = \ln 2/2$; prey carrying capacity, $K = 800$; maximum birth rates of predators 1 and 2, $m_1 = 1.3 \cdot \ln 2$; $m_2 = 0.48 \cdot \ln 2$; $m_2/y_2 = 10 \cdot \ln 2$; death rates of predators 1 and 2, $d_1 = \ln 2/2$; $d_2 = \ln 2/10$. Initial values: number of predator 1, $x_1 = 21.45$; number of predator 2, $x_2 = 21.24$; number of prey, $S = 42.82$.

ators 1 and 2 are able to coexist. For K values to the left of curve 5, predator 1 wins; whereas for K values to the right of curve 6, predator 2 wins; and K values in between permit coexistence. Line 7 marks the largest possible value of a_1 consistent with the restriction that $\lambda_1 < \lambda_2$; for a_1 greater then this value, predator 2 wins because predator 2 now has the smaller λ.

Figures 1A through 1F show the effect of decreasing the difference between b_2 and b_1 of the respective predators. When $b_2 - b_1$ is large, λ_2 is small; and predator 2 wins over most of the parameter space (Fig. 1A). In this case, coexistence is possible only if predator 1 has a very small half-saturation constant. As $b_2 - b_1$ decreases, λ_2 increases, and the coexistence region expands. Note, however, that as $b_2 - b_1$ approaches 0, line 3 approaches the horizontal, and the coexistence region is flattened to 0 against line 7. When $b_1 = b_2$, predator 1 wins for all $K > \lambda_1$ and $\lambda_1 < \lambda_2$. The boundary curves for the coexistence region (curves 5 and 6) appear to be asymptotic to the x-axis ($a_1 = 0$) with increasing K.

The width of the band of K values permitting coexistence increases sharply with an increasing difference in the half-saturation constants for the 2 predators (Fig. 2). Thus, the greater the disparity in predator affinity for prey, the greater is the latitude for variation in prey carrying capacity that will permit coexistence. For fixed differences in half-saturation constants, the width of the coexistence region is also greater for small differences in intrinsic rates of the 2 predators. Note, however, that when $b_2 - b_1$ is small, a small change in a_1 or a_2 makes a big difference in the width of the coexistence region.

In the coexistence region, the predators persist only in permanent periodic oscillations. They can coexist at a stationary equilibrium only if both λ's are precisely equal. Figures 3A and 3B illustrate the limiting periodic behavior of the predators coexisting at $K = 1100$ for the case shown in Fig. 1D, with $a_1 = 200$. If the carrying capacity is reduced, and all other parameters are left unchanged, a point is reached where predator 2 loses to predator 1. In Fig. 4, K has been reduced to 500, and predator 1 wins. The outcome is not periodic behavior, however, because K is to the left of line 4, which marks the boundary between oscillatory and nonoscillatory solutions. Similarly, if K is increased to a value exceeding $\approx$1470, predator 2 wins (Fig. 1D). Figures 5A and 5B illustrate a case in which

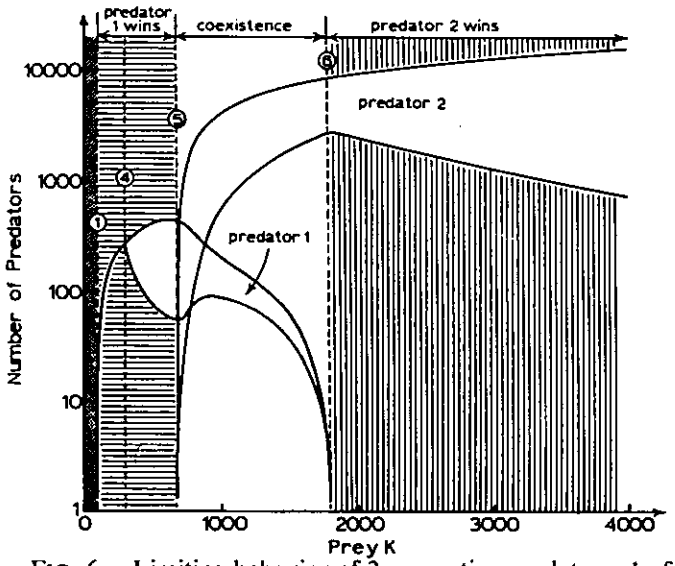

FIG. 6. Limiting behavior of 2 competing predators, 1 of which is a "K-strategist" (predator 1) and the other of which is an "r-strategist," preying upon a single prey population. Outcome as a function of prey carrying capacity, K, for the case illustrated in Fig. 1H with the half-saturation constant for predator 1, $a_1 = 100$. Shaded and hatched areas and numbered lines are coded as indicated in the legend and caption for Fig. 1. Lines for predators 1 and 2 indicate the periodic maximal and minimal population sizes in the limiting oscillations.

predator 2 wins, although for a different set of parameters than illustrated in Fig. 1D.

To illustrate more clearly how the solution changes with increasing prey carrying capacity, we have plotted the periodic maximal and minimal numbers of predators 1 and 2 as K increases through the coexistence region. Figure 6 represents a cross section of Fig. 1H for $a_1 = 100$. For increasing K, the behavior of the solution can be described as follows: For $K <$ 100 (line 1), neither predator survives (insufficient prey). For $100 < K < 300$ (between lines 1 and 4), predator 1 wins, and its numbers approach a constant equilibrium. For $300 < K < \approx 675$ (between line 4 and curve 5), predator 1 again wins, but its numbers become permanently oscillatory. For $\approx 675 < K < \approx 1780$ (between curves 5 and 6), predators 1 and 2 coexist in permanent oscillations. Finally, for $K > \approx 1780$ (curve 6), predator 2 wins, and its numbers are permanently oscillatory. Note that predator 2, the species with the higher intrinsic rate of increase and half-saturation constant, exhibits oscillations of much larger amplitude than those of predator 1, except when K is near curve 5. Not graphed is the behavior of the prey population, which approaches constant numbers for K to the left of line 4, and is permanently oscillatory for K to the right of line 4. Although it remains unproven analytically, it is clear from the numerical analysis that these periodic oscillations are limit cycles.

DISCUSSION

This paper is a mathematical analysis of the behavior of a model of 2 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 4 parameters: K, the carrying capacity of the prey, and the parameters of the ith predator; a_i, the half-saturation constant; b_i, the ratio of maximal birth rate to death rate; and λ_i. (The "λ" parameter has been symbolized by Rosenzweig [1973] with the letter "J." Also the Greek letter χ has appeared in the literature to symbolize the half-saturation constant.) λ_i is a particularly important parameter. Recall that λ_i is the product of the ith predator's half-saturation constant times the ratio of the predator's death rate to its intrinsic rate of increase: $\lambda_i = a_i(d_i/r_i)$. This number is the break-even concentration of prey for the ith predator's $dx_i/dt = 0$ isocline in the $S - x_i$ plane. A predator with a small half-saturation constant, low death rate, and high intrinsic rate of increase (small λ) should be a tough competitor to beat.

In fact, 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 become extinct (Hsu et al. 1977). The surviving species and its resource 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. As in the constantly supplied resource case, the predators' λ parameters are important; but, in addition, K, a_i, and b_i must be considered to determine the outcomes of interspecific competition between the predators.

We have been concerned with answering the question: Under what conditions will neither, 1, or both species of predator survive or die out? We divide our results into 3 general cases: case I, neither predator can survive (even without competition) on this resource; case II, the first predator can survive on this resource but the second cannot; case III, each predator can, in the absence of competition, survive on this resource.

Table 1 summarizes the 3 principal cases. Note that we have omitted reference in the table to all cases which can be obtained by symmetry—cases obtainable by simply interchanging all predator subscripts. In general, we have presented the cases in which predator 1 wins.

Case I: This represents the case in which neither predator can survive on the prey, regardless of the presence or absence of its rival. This situation can arise for 1 of 2 reasons: either the predator's intrinsic rate of increase is negative or 0 ($b_i \leq 1$), or else the prey carrying capacity is below the break-even density for the predator. In either event, both predators be-

TABLE 1. Classification of outcomes for 2 competing predators. See text for explanation of symbols

Case	Prey	Predator 1	Predator 2
I: $\lambda_i > K$ or $b_i \leq 1$, $i = 1,2$.	Approaches K	Dies out	Dies out
II: $\lambda_1 < K$, $b_1 > 1$, $\lambda_2 \geq K$ or $b_2 \leq 1$.			
A. $K < a_1 + 2\lambda_1$	Approaches λ_1	Approaches $x_1^* > 0$	Dies out
B. $K > a_1 + 2\lambda_1$	Periodic	Periodic	Dies out
III: $0 < \lambda_1 < \lambda_2 < K$, $b_i > 1$, $i = 1,2$			
A. $K < a_1 + 2\lambda_1$			
1. $b_1 \geq b_2$	Approaches λ_1	Approaches $x_1^* > 0$	Dies out
2. $a_1 < a_2$, $b_1 < b_2$			
a) $K < \frac{a_2b_1 - a_1b_2}{b_2 - b_1}$	Approaches λ_1	Approaches $x_1^* > 0$	Dies out
b) $K > \frac{a_2b_1 - a_1b_2}{b_2 - b_1}$			
$(a_1, K) \in Q_1$	Approaches λ_1[†]	Approaches $x_1^* > 0$[†]	Dies out[†]
B. $K > a_1 + 2\lambda_1$			
1. $b_1 \geq b_2$	Periodic	Periodic	Dies out
2. $a_1 < a_2$, $b_1 < b_2$			
a) $K < \frac{a_2b_1 - a_1b_2}{b_2 - b_1}$	Periodic	Periodic	Dies out
b) $K > \frac{a_2b_1 - a_1b_2}{b_2 - b_1}$			
i) $(a_1, K) \in Q_1$	Periodic[†]	Periodic[†]	Dies out[†]
ii) $(a_1, K) \in Q_2$	Periodic[†]	Periodic[†]	Periodic[†]
iii) $(a_1, K) \in Q_3$	Periodic[†]	Dies out[†]	Periodic[†]

[†] These outcomes are known from numerical results only.

come extinct, and the prey population equilibrates at K.

Case II: This situation is readily understood from the outcome in Case I. One of the predators (species 2 in the case tabled) cannot survive on the prey no matter what its rival does, but the rival (species 1) can survive when grown alone on the prey. In the limit, this case becomes a 1 predator–1 prey system. In order to understand the full behavior of the 2-predator system, it was therefore necessary to analyze the 1-predator case. Our analysis of the 1 predator–1 prey case is global, and is a more general treatment than any of which we are aware in the literature. We therefore digress briefly from the 2-predator system to discuss the limiting behavior of the 1 predator–1 prey system.

The solution curves representing the outcomes for Case II can be plotted in the S-x plane (Rosenzweig and MacArthur 1963), where S is prey density (x-axis) and x is the density of the winning predator (y-axis). The isocline for the prey $S = 0$ is an inverted parabola intersecting the S-axis at K, and reaching a maximum at $(K - a)/2$, where a is the predator's half-saturation constant. The isocline for the predator $x = 0$ is a vertical line intersecting the S-axis at λ. There are 2 outcomes for Case II, depending upon the location of λ in relation to the maximum on the prey isocline.

If $\lambda > (K - a)/2$, the predator-prey trajectory is a damped oscillation to an equilibrium point (Case IIA). If $\lambda < (K - a)/2$, the trajectory is permanently cyclic. We conjecture that for these equations there is a unique, asymptotically stable limit cycle, but proof of this conjecture is presently unavailable (the counter-example to the result of May [1972] found by Albrecht et al. [1974] illustrates that this can be a delicate question). Biologically, however, it is an irrelevant technicality whether the solution is really a stable limit cycle or is a split, semistable limit cycle: the limiting behavior in either event is permanently periodic.

Any of the 1-predator systems can be made to exhibit permanent, periodic solutions merely by increasing the carrying capacity of the prey population sufficiently. May (1973) has remarked that increasing K is like gradually relaxing the density-dependent restraint on growth of the prey population at low densities, thereby permitting faster recovery of the prey population after the predator crashes.

Rosenzweig (1971) labelled the tendency of preda-

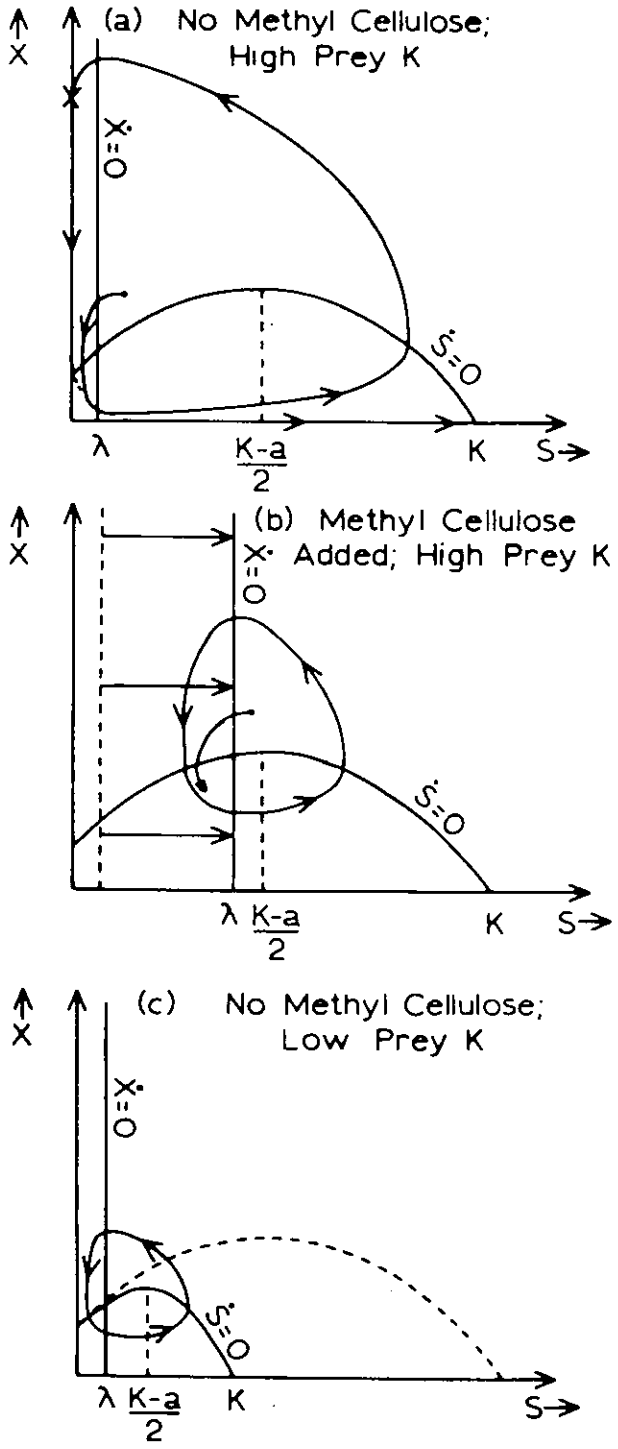

FIG. 7. Illustration on the s-x plane of the results of Luckinbill's (1973) experiment on Didinium–Paramecium predator–prey systems. (a) No methyl cellulose added, high prey carrying capacity (K), so $\lambda \ll (K - a)/2$, where λ is the break-even prey density for the predator and a is the predator's half-saturation constant. Result: limiting periodic solution is unrealizable—the predator dies out and the prey grow to K; (b) Methyl cellulose added (decreasing predator-prey encounter rate), high prey K, so λ increases to nearly $(K - a)/2$. Result: limiting perodic solution is realizable because prey are not driven to extremely low values; (c) No methyl cellulose added, but prey K reduced substantially, reducing $(K - a)/2$ to nearly λ. Result: limiting periodic solution again realizable, but with much reduced amplitude. Predator never builds to levels high enough to drive prey to extremely low densities.

tor–prey systems to become increasingly oscillatory with increases in K, the "paradox of enrichment," but he erroneously concluded that such oscillations are relaxed, leading to the extinction of the predator, or of both predator and prey. Gilpin (1972) found "limit cycles" instead of relaxed oscillations when $\lambda < (K - a)/2$, and attributed Rosenzweig's (1971) result to insufficiently low error bounds in the numerical simulation. We have provided a rigorous proof of Gilpin's (1972) numerical result (for 2-dimensional periodic solutions).

However, we agree with Gilpin (1972) that, biologically, Rosenzweig (1971) may often be right in predicting extinctions when K is large. Gilpin (1972) found cases in which the numerical solutions gave unrealistically small population sizes to predator and prey at the cycle lows—sizes often <1 individual. In such cases the populations of organisms in question would be expected to die out. Further detailed numerical studies would be required to establish precisely what parameter values produce these unrealistically low values. It is clear, however, that the smaller λ becomes in relation to $(K - a)/2$, the larger is the amplitude of the limit cycle, and the deeper and more prolonged the lows become. May (1972, 1973) obtained an estimate of the ratio of the predator's minimum population and the predator's mean population for a very similar predator–prey model exhibiting a limit cycle. He showed that this ratio is approximately equal to $\exp[-\alpha(K/S^*)]$, where α is a constant near unity, K is the prey carrying capacity, and S^* is mean prey population size. If (K/S^*) is large, then this ratio is extremely small, and the predator population falls below 1 individual, and therefore becomes extinct, before the minimum of the limit cycle is reached. In our system, if the predator is a very efficient hunter (has a small half-saturation constant) and has a high intrinsic rate of increase, then λ is small, and the predator can drive the prey population to very low levels. The predator will then crash to very low levels itself. If this level is <1 individual, the limit cycle is biologically unrealizable; and the predator becomes extinct. This discrepancy between the model and nature only arises when the populations of predator or prey are very small, and is due to the model's assumption that population size is a continuous variable.

It is of interest to relate our findings on the 1 predator–1 prey system to the experimental results of Luckinbill (1973), who studied a predator–prey system consisting of the ciliate protozoans, *Didinium nasutum* and *Paramecium aurelia*. Previously, Gause (1934) had studied this system, but he was unable to prevent *Didinium* from consuming all the *Paramecium* without providing some sort of physical refuge for the prey. Luckinbill (1973) showed that he could significantly prolong the coexistence of predator and prey either by adding methyl cellulose to the culture me-

dium, or by reducing the bacterial food supply to the *Paramecium*. The methyl cellulose increased the viscosity of the medium, thereby reducing the rate of encounters between predator and prey. The reduction in bacterial food supply for the *Paramecium* reduced the carrying capacity for the prey species. Our results provide a consistent explanation of these experimental findings. The explanation lies in the effect of the experimental manipulations on the relative positions of the predator ($dx/dt = 0$) isocline and the peak of the prey ($dS/dt = 0$) isocline. Consider first the control case in which no methyl cellulose has been added, and the carrying capacity K is high for the *Paramecium* prey (Fig. 7a). The predator isocline, located at $S = \lambda$, is at a very low value relative to $(K - a)/2$, the peak in the prey isocline. The parameter λ is small because the half-saturation constant and death rate of *Didinium* are small in comparison with its intrinsic rate of increase. *Didinium* tends to divide and become smaller in the absence of food, so its death rate is very low. The result is an approach to a limit cycle which is of very large amplitude. For the reasons given above, however, biologically, the limit cycle is not realizable, and the prey are driven to extinction.

Now suppose methyl cellulose is added to the culture medium. Immediately, the effect is to lower the encounter rate between *Didinium* and *Paramecium* because swimming rates are reduced more in *Didinium* than in *Paramecium* due to differences in cell shape. Only the encounter rate is affected; handling time remains unchanged. Recall from the Introduction that the half-saturation constant is the inverse of the product of encounter rate, c, and handling time, h. Hence, any reduction in encounter rate produces an increase in the predator's half-saturation constant, which produces an increase in λ. The result is that λ becomes more nearly equal to $(K - a)/2$. When λ is increased (Fig. 7b), the predator and prey still oscillate, but the limit cycle has a much-reduced amplitude, and the chance of prey extinction is much reduced. This is precisely what happened in Luckinbill's (1973) experiments.

Finally, suppose that no methyl cellulose is added, but the Cerophyl medium used to grow the bacterial food of the *Paramecium* is reduced. This will have the effect of reducing K and the value of prey density at which the peak occurs on the prey isocline (Fig. 7c). This happens because the *Paramecium* carrying capacity is reduced, while the half-saturation constant for *Didinium* is unchanged. The effect of lowering K is therefore to make λ closer to the peak, thereby again reducing the amplitude of the predator–prey cycles as well as the chance of prey extinction.

Luckinbill (1974) also obtained greater persistence and smaller cycle amplitudes merely by increasing the volume of his culture. The total amount of Cerophyl added was kept the same. This volume increase had the effect of simultaneously lowering the prey carrying capacity (calculated as a density of number of *Paramecium* supportable/ml) and lowering the predator's encounter rate. Both of these factors should increase λ relative to $(K - a)/2$.

From the results we have presented, it is tempting to predict that if culture volumes had been increased still further, a point would have been reached where λ was greater than the peak value of $(K - a)/2$; and *Didinium* and *Paramecium* would have achieved a stable equilibrium. This outcome would be expected except for the fact that *Didinium* exhibits a short time lag in response to changes in *Paramecium* abundance. We have not yet studied time lags in the model given by (2.1), but in general the effect of time lags is to increase the oscillatory tendencies of a system. Such time lags might also give rise to outcomes in which the *Didinium* drive the *Paramecium* to extinction.

In the Introduction we raised the question of how often one might expect to find predator–prey limit cycles in nature. The likelihood is increased if the predator in question derives its food solely or principally from 1 prey species. It is further increased if the predator is an effective hunter at low prey density (half-saturation constant small) and has a high intrinsic rate of increase. It is further increased if the prey species is capable of becoming very abundant if predation pressure is relaxed.

The predator–prey model developed here assumed density-independent mortality for the predators, but we predict that incorporation of density-dependence in the predator death rates will have little qualitative effect on our conclusions. Rosenzweig (1971) and Gilpin (1972) numerically studied models with density-dependent predator death rates, and the only effect was to shift slightly the position of the peak in the prey isocline.

We return now to Table 1 and the discussion of the 2-predator system.

Case III: This case represents the most interesting and potentially complex situation of the 2 predator-1 prey system. In this case, both predators can handily survive when grown alone on the prey. This condition is met when the prey carrying capacity exceeds the value of λ for each predator. Consider first the case in which $\lambda_1 < \lambda_2$. In the case of a resource supplied at a constant rate, we have proven that $\lambda_1 < \lambda_2$ would be sufficient to guarantee that predator 1 wins and predator 2 dies out. However, when the prey regenerates logistically, this relationship between the λ is neither a necessary nor a sufficient condition for survival of predator 1 and extinction of predator 2.

The principal result of our numerical simulation was to locate the 2 curves 5 and 6 in Figs. 1A–1H referred to in the discussion above. Designate the region below line 7 in the $a_1 - K$ parameter space (for fixed a_2, b_1, b_2) to the left of curve 5 as Q_1, the region between

curves 5 and 6 as Q_2, and the region to the right of curve 6 as Q_3. The results known only by simulation are marked in the table with the symbol $\perp$. (These, of course, are candidates for future theorems.)

In the subcase IIIA, predator 1 wins and approaches a constant value. In the first instance, species 1 wins because it has the lower half-saturation constant as well as the higher intrinsic rate of increase of the 2 competitors. It is interesting that species 1 also wins even when it has a higher half-saturation constant, so long as λ_1 is $< \lambda_2$.

Coexistence arises in subcase IIIB(2)b(ii) in which species 1 not only has the lower half-saturation constant, but also the lower birth rate/death rate ratio of the 2 predators. Analytically, we have shown only that predator 1 persists in case that $K < a_2 + 2\lambda_2$, but we have not been able to prove that coexistence is possible. However, we have unequivocal numerical results which justify this claim (see below), confirming the findings of Koch (1974). (See Fig. 3.)

All of the cases of coexistence we found had periodic solutions. (We are aware, of course, that numerically one might not be able to distinguish periodic and almost periodic solutions.) The proof of Theorem 3.5 of Hsu et al. (1977) shows that limiting constant behavior is possible only if x_1 wins. The numerical experiments show that predator 2, the species with higher half-saturation constant and intrinsic rate of increase, loses when the prey carrying capacity is too low, wins when K is high, and coexists with predator 1 at intermediate values of K, for fixed values of λ_1 and λ_2. *In general, we predict that whenever* $\lambda_1 < \lambda_2 <$ K, $a_1 < a_2$, *and* $b_1 < b_2$, *there must exist a range of* K *values for which coexistence between the competing predators results. Indeed, we predict that the coexistence region can be made arbitrarily large by appropriate choice of parameters.*

It should be noted that this coexistence results merely from the dynamics of growth of the predators and prey, and to characteristics of the predators' functional responses, and not from any spatial heterogeneity or from any externally applied, periodic forcing function; the system is completely autonomous.

It is interesting to relate these results to published speculations and conclusions about competitive coexistence between species. When the predators have nonlinear functional responses and the prey population has density-dependent (nonlinear) growth, dynamic coexistence between competing predators is possible (McGehee and Armstrong 1976). This result has been missed by most theoretical studies of competition because of linear assumptions about functional responses and a lack of treatment of resource dynamics (Armstrong and McGehee 1976). Also, typically only equilibrium conditions have been examined, with the result that periodic solutions may be missed entirely.

In an early work, MacArthur (1960) spoke of "opportunist" and "equilibrium" species, a concept which he later refined in the notions of "r-strategist" and "K-strategist" (MacArthur and Wilson 1967). In resource terms, we can redefine an r-strategist as a species with a high maximal intrinsic rate of increase, but a species of poor competitive ability at low resource density. The r-strategist is capable of growing at its maximal rate only at high resource densities. A K-strategist, however, has only a low maximal intrinsic rate of increase, but it is capable of growing at its maximal rate at very low levels of resource.

MacArthur (1958) argued that opportunist species could coexist with equilibrium species, provided that they could predictably find communities in which resource abundances were locally superabundant in space or time. Hutchinson (1961), however, in considering why there were so many coexisting species of plankton, rejected as unlikely that the community was composed of opportunistic species. He felt that chance extinctions were very likely to be much greater for opportunistic species, thereby reducing their importance and frequency in the community. However, Hulbert (1970) found that many planktonic species in the Sargasso came and went with the seasons, showing huge fluctuations in density; but that other species showed hardly any seasonal change in abundance, having little response to increases or decreases in the seasonal species. Stewart and Levin (1973) then showed analytically that coexistence was possible for 2 species sharing a common limiting resource in a periodic environment in which resources fluctuate from high to low levels. The resource was depleted at the end of each season, and the populations of plankton were restarted in the next season by means of small seed populations. Although they did not refer to the coexisting species in terms of r-strategist and K-strategist, it is interesting that the numerical case of coexistence illustrated (Fig. 1, p. 177) fits our requirement for $a_1 < a_2$ and $b_1 < b_2$ (note a different notational use of a and b in the Stewart and Levin [1973] paper).

Perhaps it is somewhat premature to judge the importance of coexistence of r- and K-strategists by the method proposed. In the deterministic case studied here, with fixed K, it is not at all clear that there is an upper limit to the number of dynamically coexisting predator species (Armstrong and McGehee 1976). However, we speculate that the parameter space which allows for the successive additions of predator species supported by the same prey resource gets rapidly smaller with each new predator added. In nature, we suspect that the number of species coexisting on a single resource is severely limited by stochastic forces. We have noted that the coexistence region depends critically upon the size of the carrying capacity of the prey population, a number much more subject to rapid change than the evolutionarily adjusted, functional-response and population-growth parameters of

the predators. Thus, extending the argument of Hutchinson (1961), a fluctuation of K too high or too low for too long could result in the extinction of 1 or more of the predator species.

Nevertheless, we can say that, in nature, 2 species are probably rarely limited forever and anon by a single resource. In the context of multiple resources, it seems likely that a diversity of life-history patterns across the r–K continuum would allow for a greater number of species to coexist than otherwise. Indeed, it might represent 1 of the principal ways by which species can outnumber their limiting resources.

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