Some of the properties of the equations describing two predators competing for the same prey are analyzed. In particular it is found that, under certain conditions, both predators can survive, with or without oscillations in the prey population.

1. Introduction. In previous papers I have examined the behavior of three species competing for the same resource (Rescigno, 1968) or forming a predator-prey chain (Rescigno and Jones, 1972). Here I plan to discuss the properties of two predators competing for the same prey; this problem is important not per se, but for the light it sheds on the much discussed "Competitive Exclusion Principle" (Volterra, 1927; Hardin, 1960; Rescigno and Richardson, 1965; Levin, 1970) and because it can be solved using only elementary mathematical methods.

2. Rules defining the Predator–Prey System. The present predator-prey system is represented by the equations

\[ \dot{N}_1 = N_1K_1(N_1, N_2, N_3), \]
\[ \dot{N}_2 = N_2K_2(N_1, N_2, N_3), \]
\[ \dot{N}_3 = N_3K_3(N_1, N_2, N_3), \]

where \( N_1 \) is the number of preys, \( N_2 \) and \( N_3 \) the numbers of individuals of the two predator species, \( K_1, K_2, K_3 \) are continuous functions of their arguments.
Besides the usual hypotheses implicit in this kind of equations (Rescigno and Richardson, 1967, 1973) the following hypotheses specifically apply to this system.

(a) If predators and prey are both in small number, the prey multiplies, being unhindered by predators.

(b) The prey cannot multiply over a certain population size, even in the absence of predators, because of intraspecific competition.

(c) If there are too many predators, the prey cannot multiply.

(d) The multiplication of the prey is slowed by an increase in the number of predators.

(e) For a constant predator/prey ratio, the multiplication of the prey is slowed by an increase of the population sizes, because the encounters are more frequent.

(f) If there are not enough prey, the predators cannot multiply.

(g) The multiplication of the predators is slowed by an increase in their number.

(h) For a constant predator/prey ratio, the multiplication of the predators is accelerated by an increase of the population sizes, because the encounters are more frequent.

From the above hypotheses, the following properties of functions $K_1$, $K_2$, $K_3$ derive.

(1) $K_1(0, 0, 0) > 0$, because of hypothesis (a).

(2) There exists an $A > 0$ such that $K_1(A, 0, 0) = 0$, because of hypothesis (b).

(3) There exists a $B > 0$ such that $K_1(0, B, 0) = 0$, because of hypothesis (c).

(4) There exists a $C > 0$ such that $K_1(0, 0, C) = 0$, because of hypothesis (e).

(5) $\frac{\partial K_1}{\partial N_2} < 0$, because of hypothesis (d).

(6) $\frac{\partial K_1}{\partial N_3} < 0$, because of hypothesis (d).

(7) $\frac{dK_1}{dR} < 0$, where $R$ is the direction of a straight line of equations $N_1/N_2 = \text{constant}$, $N_3 = \text{constant}$, because of hypothesis (e).

(8) $\frac{dK_1}{dS} < 0$, where $S$ is the direction of a straight line of equations $N_1/N_3 = \text{constant}$, $N_2 = \text{constant}$, because of hypothesis (e).

(9) $\frac{\partial K_2}{\partial N_3} = 0$, because one predator does not depend directly on the other; therefore we can write simply $K_2(N_1, N_2)$.

(10) $\frac{\partial K_3}{\partial N_2} = 0$, for the reason above; therefore we can write $K_3(N_1, N_3)$.

(11) There exists a $D > 0$ such that $K_2(D, 0) = 0$, because of hypothesis (f).

(12) There exists an $E > 0$ such that $K_3(E, 0) = 0$, because of hypothesis (f).

(13) $\frac{\partial K_3}{\partial N_2} < 0$, because of hypothesis (g).

(14) $\frac{\partial K_3}{\partial N_3} < 0$, because of hypothesis (g).
(15) \( \frac{dK_2}{dR} > 0 \), because of hypothesis (h).
(16) \( \frac{dK_3}{dS} > 0 \), because of hypothesis (h).

3. Geometrical Interpretation. In Figure 1 properties 2, 3, 5, 7 have been used to draw the line of equations \( K_1 = 0, N_3 = 0 \); properties 11, 13, 15 for the line of equations \( K_2 = 0, N_3 = 0 \); properties 10, 12 for the line of equations \( K_3 = 0, N_3 = 0 \).

At the origin, \( K_1 > 0 \) (property 1), \( K_2 < 0 \) (property 15), \( K_3 < 0 \) (property 16).

![Figure 1](image)

Increasing the value of \( N_3 \), the line \( K_1 = 0 \) shown in Figure 1 moves toward smaller values of \( N_1 \) and \( N_2 \) (properties 6, 8), the line \( K_2 = 0 \) does not change (property 9), the line \( K_3 = 0 \) moves with a parallel motion toward larger values of \( N_1 \) (property 14). For \( N_3 = C \), the line \( K_1 = 0 \) is reduced to the point \( N_1 = 0, N_2 = 0 \) (property 4).

As Figure 1 shows, for \( N_3 = 0 \) the lines \( K_2 = 0 \) and \( K_3 = 0 \) have a point \( X \) in common if \( D < E \); (if \( D = E \), point \( X \) coincides with \( D \)). By increasing \( N_3 \), this point moves along the line \( K_2 = 0 \) toward larger values of \( N_1 \) and \( N_2 \); if \( X \) lies between line \( K_1 = 0 \) and the origin, i.e. if \( P_1 > E \), there exists a point \( Z \) where \( K_1 = 0, K_2 = 0, K_3 = 0 \); if \( X \) lies on line \( K_1 = 0, Z \) coincides with \( X \).

The case \( D > E \) can be reduced to the case above, without loss of generality, by switching \( N_2 \) and \( N_3 \).

4. Singular Points. The three time derivatives \( \dot{N}_1, \dot{N}_2, \dot{N}_3 \) are simultaneously zero in the following cases.

\( N_1 = N_2 = N_3 = 0 \). The origin. At this point \( K_1 > 0, K_2 < 0, K_3 < 0 \): the prey always survives.

\( K_1 = N_2 = N_3 = 0 \). Point \( A \). We must distinguish two cases.
A < D < E. Here $K_2 < 0, K_3 < 0$; $A$ is a stable node: only the prey survives.

$A > D$. Here $K_2 > 0$; $A$ is not a stable point.

$N_1 = K_2 = N_3 = 0$. Impossible.

$N_1 = N_2 = K_3 = 0$. Impossible.

$N_1 = K_2 = K_3 = 0$. Impossible.

$K_1 = K_2 = N_3 = 0$. Point $P$ (see Figure 1). We must distinguish two cases.

$P_1 < E$. Here $K_3 < 0$; $P$ may be a center, a node or a focus, either stable or unstable, as in the case considered by Kolmogoroff (1936).

$P_1 > E$. Here $K_3 > 0$; $P$ is not a stable point.

$K_1 = N_2 = K_3 = 0$. This point exists only if $E < A$; because of our hypothesis that $D < E$, at this point $K_3 > 0$, therefore it is not a stable point.

$K_1 = K_2 = K_3 = 0$. Point $Z$. As seen in the previous section, this point exists only if $E < P_1$; in this case neither $A$ nor $P$ are stable points.

5. Behavior of the System near point $Z$. The Jacobian determinant of this system is

\[
\begin{vmatrix}
N_1 K_1 + N_1 \frac{\partial K_1}{\partial N_1} & N_1 \frac{\partial K_1}{\partial N_2} & N_1 \frac{\partial K_1}{\partial N_3} \\
N_2 \frac{\partial K_1}{\partial N_1} & N_2 K_2 + N_2 \frac{\partial K_2}{\partial N_2} & 0 \\
N_3 \frac{\partial K_3}{\partial N_1} & 0 & N_3 K_3 + N_3 \frac{\partial K_3}{\partial N_3}
\end{vmatrix}
\]

and its characteristic equation at point $Z$ is

\[
\lambda^3 - (Z_1 K_{11} + Z_2 K_{22} + Z_3 K_{33}) \lambda^2 + [Z_1 Z_2 (K_{11} K_{22} - K_{12} K_{21})
+ Z_1 Z_3 (K_{11} K_{33} - K_{13} K_{31}) + Z_2 Z_3 K_{22} K_{33}] \lambda
- Z_1 Z_2 Z_3 (K_{11} K_{22} K_{33}) = 0,
\]

where $Z_1, Z_2, Z_3$, are the coordinates of point $Z$, while $K_{ij}$ is the value of $\partial K_i / \partial N_j$ at point $Z$ ($i, j = 1, 2, 3$).

The characteristic equation can be written

\[
(\lambda - Z_1 K_{11})(\lambda - Z_2 K_{22})(\lambda - Z_3 K_{33}) = (Z_1 Z_2 K_{12} K_{21} + Z_1 Z_3 K_{13} K_{31}) \lambda
- Z_1 Z_2 Z_3 (K_{12} K_{21} K_{33} + K_{13} K_{22} K_{31});
\]
its three roots are given, as shown in Figure 2, by the intersections of a cubic (the left hand side of the equation) with a straight line (the right hand side).

Because of the constraints shown in Table I, the cubic intersects the abscissa at two points on the left of the origin and at a point that can be either on the left or on the right. The straight line intersects both abscissa and ordinate on negative points. With a proper choice of the parameters the three intersections will all have negative values of $\lambda$ as Figure 2 shows; with a value of $|Z_1Z_2K_{12}K_{21} + Z_1Z_3K_{13}K_{31}|$ large enough there will be only one intersection, at a negative value of $\lambda$; with a value of $Z_1K_{11}$ large enough and of $|Z_1Z_2K_{12}K_{21}$
+Z₁Z₃K₁₈K₃₁| small enough, there will be two intersections at negative values of λ and one at a positive value of λ.

Therefore point Z can be either a node or a focus, and either stable or unstable.

We can now conclude that the necessary and sufficient condition for the survival of all three species is the existence of point Z. Properties 2, 3, 4, 11, 12 guarantee that the size of all species is bounded.

6. Discussion. Kock (1974) has shown that two predators utilizing the same prey can coexist, but not in a steady-state situation; here I have shown that with the inclusion of hypothesis (g), and thence properties 13 and 14, two predators utilizing the same prey can coexist with or without oscillations.

Indeed, if \( \partial K₂/\partial N₂ = 0 \), the line of equation \( K₂ = 0, N₃ = 0 \) would be parallel to the \( N₂ \) axis, and either point \( X \) would not exist, or, in the special case \( D = E \), the above line would coincide with the line of equation \( K₃ = 0, N₃ = 0 \).

On the other hand all conclusions reached in sections 3, 4, 5 are valid if \( \partial K₂/\partial N₂ < 0 \) at least for \( N₂ \) large enough, and \( \partial K₃/\partial N₃ < 0 \) at least for \( N₃ \) large enough; in other words, hypothesis (g) is required only for population densities above a certain value.

As seen in section 5, the existence of oscillations in the population densities depends on the values of the functions \( K₁, K₂, K₃ \), and of their derivatives, in a neighborhood of point Z, while the number of species surviving depend only on the values of those functions on the planes \( N₁ = 0, N₂ = 0, N₃ = 0 \).

I intend to show in a following paper how those considerations can be extended to other ecological associations and be interpreted in the light of the Competitive Exclusion Principle.

LITERATURE
