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# ON MAY'S PREDATOR-PREY MODEL

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For May's 2-predator 2-prey model, a criterion has been developed to decide as to which predator and which prey species will disappear. When the non-zero equilibrium position does not exist, the criterion depends only on the parameters of the model. However when this position exists but is unstable, the disappearing species will also depend on the initial conditions. Some of the results have been generalised to $n$-predator $n$-prey model. The possibility of existence of systems for which the number of predator and prey species are not equal has been considered. Some examples of these with conservative oscillations are given.

## 1. INTRODUCTION

May (1971, 1973) has given the $n$-predator $n$-prey model

$$\left.\begin{aligned} \frac{dH_i}{dt} &= H_i(t)\,[a_i - \sum_{j=1}^{n} \alpha_{ij} P_j(t)], \quad i = 1, 2, \ldots, n \\ \frac{dP_i}{dt} &= P_i(t)\,[-b_i + \sum_{j=1}^{n} \beta_{ij} H_j(t)], \quad i = 1, 2, \ldots, n \end{aligned}\right\} \quad \ldots(1)$$

as a generalisation of Lotka-Volterra (Lotka 1925) one-prey one-predator model

$$\left.\begin{aligned} \frac{dH}{dt} &= H(t)\,[a - \alpha P(t)] \\ \frac{dP}{dt} &= P(t)\,[-b + \beta H(t)] \end{aligned}\right\} \quad \ldots(2)$$

and has discussed the stability of the equilibrium position in which the populations of all the $2n$ species are non-zero. He showed that while this non-zero equilibrium position (nzep) is always in neutral equilibrium for $n = 1$, it may be either in neutral equilibrium or in unstable equilibrium when $n > 1$. When the equilibrium is unstable, in general one predator and one prey species will disappear and we shall be left with a system with $(n - 1)$ predator and $(n - 1)$ prey species.

The following questions naturally arise:

(i) When the nzep is unstable, which of the predator species and which of the prey species will disappear ?

(ii) Will the particular species which vanish be determined by initial conditions or ecological parameters or both ?

(iii) What happens if nzep does not exist i.e. if our attempt to find the equilibrium values of the population sizes gives rise to negative values for them ?

We first discuss these questions for $n = 2$ and then generalise the results for general values of $n$.

## 2. The Possible Equilibrium Positions When $n = 2$

When $n = 2$, the model (1) becomes

$$\left.\begin{aligned} \frac{dH_1}{dt} &= H_1(t)\,[a_1 - \alpha_{11}P_1(t) - \alpha_{12}P_2(t)] \\ \frac{dH_2}{dt} &= H_2(t)\,[a_2 - \alpha_{21}P_1(t) - \alpha_{22}P_2(t)] \\ \frac{dP_1}{dt} &= P_1(t)\,[-b_1 + \beta_{11}H_1(t) + \beta_{12}H_2(t)]; \\ \frac{dP_2}{dt} &= P_2(t)\,[-b_2 + \beta_{21}H_1(t) + \beta_{22}H_2(t)]. \end{aligned}\right\} \quad \ldots(3)$$

The following six positions of equilibrium are possible

(i) $\bar{H}_1 = 0,\ \bar{H}_2 = 0,\ \bar{P}_1 = 0,\ \bar{P}_2 = 0$ ...(4)

(ii) $\bar{H}_1 = 0,\ \bar{H}_2 = \dfrac{b_2}{\beta_{22}},\ \bar{P}_1 = 0,\ \bar{P}_2 = \dfrac{a_2}{\alpha_{22}}$ ...(5)

(iii) $\bar{H}_1 = \dfrac{b_1}{\beta_{11}},\ \bar{H}_2 = 0,\ \bar{P}_1 = \dfrac{a_1}{\alpha_{11}},\ \bar{P}_2 = 0$ ...(6)

(iv) $\bar{H}_1 = 0,\ \bar{H}_2 = \dfrac{b_1}{\beta_{12}},\ \bar{P}_1 = \dfrac{a_2}{\alpha_{21}},\ \bar{P}_2 = 0$ ...(7)

(v) $\bar{H}_1 = \dfrac{b_2}{\beta_{21}},\ \bar{H}_2 = 0,\ \bar{P}_1 = 0,\ \bar{P}_2 = \dfrac{a_1}{\alpha_{12}}$ ...(8)

$$\left.\begin{aligned} &\text{(vi)}\ \bar{H}_1 = \frac{b_1\beta_{22} - b_2\beta_{12}}{\beta_{11}\beta_{22} - \beta_{12}\beta_{21}},\quad \bar{H}_2 = \frac{b_2\beta_{11} - b_1\beta_{21}}{\beta_{11}\beta_{12} - \beta_{12}\beta_{21}} \\ &\bar{P}_1 = \frac{a_1\alpha_{22} - a_2\alpha_{12}}{\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21}},\quad \bar{P} = \frac{a_2\alpha_{11} - a_1\alpha_{21}}{\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21}}. \end{aligned}\right\} \quad \ldots(9)$$

If we substitute

$$\left.\begin{aligned} A_1 &= \frac{a_1}{\alpha_{12}} - \frac{a_2}{\alpha_{22}},\ A_2 = \frac{a_2}{\alpha_{21}} - \frac{a_1}{\alpha_{11}},\ A_3 = \alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21} \\ B_1 &= \frac{b_1}{\beta_{12}} - \frac{b_2}{\beta_{22}},\ B_2 = \frac{b_2}{\beta_{21}} - \frac{b_1}{\beta_{11}},\ B_3 = \beta_{11}\beta_{22} - \beta_{12}\beta_{21} \end{aligned}\right\} \quad \ldots(10)$$

then (9) can be written as

$$\text{(vii)}\ \bar{H}_1 = \beta_{12}\beta_{21}\frac{B_1}{B_3},\ \bar{H}_2 = \beta_{11}\beta_{21}\frac{B_2}{B_3},\ \bar{P}_1 = \alpha_{12}\alpha_{22}\frac{A_1}{A_3},\ \bar{P}_2 = \alpha_{11}\alpha_{21}\frac{A_2}{A_3}, \quad \ldots(11)$$

so that this nzep exists only if $A_1$, $A_2$, $A_3$ have the same sign and also $B_1$, $B_2$, $B_3$ have the same sign i.e. when the signs of $A_1$, $A_2$, $A_3$, $B_1$, $B_2$, $B_3$ are given by one of the following:

$$(a)\ +++,\ +++\quad (b)\ +++,\ ---\quad (c)\ ---,\ +++\quad (d)\ ---,\ ---. \quad \ldots(12)$$

Now we shall assume for the present that each of $A_1$, $A_2$, $A_3$, $B_1$, $B_2$, $B_3$ is either positive or negative so that there are apparently 64 cases. However 28 of these cases cannot arise because whenever $A_1$, $A_2$ ($B_1$, $B_2$) are positive, then $A_3(B_3)$ is also positive and whenever $A_1$, $A_2(B_1, B_2)$ are negative, then $A_3(B_3)$ is also negative. This is easily seen to be true since

$$\left.\begin{aligned} A_1 > 0,\ A_2 > 0 &\Rightarrow \frac{a_1}{a_2} > \frac{\alpha_{12}}{\alpha_{22}},\ \frac{a_1}{a_2} < \frac{\alpha_{11}}{\alpha_{21}} \Rightarrow \frac{\alpha_{11}}{\alpha_{21}} > \frac{\alpha_{12}}{\alpha_{22}} \Rightarrow A_3 > 0 \\ A_1 < 0,\ A_2 < 0 &\Rightarrow \frac{a_1}{a_2} < \frac{\alpha_{12}}{\alpha_{22}},\ \frac{a_1}{a_2} > \frac{\alpha_{11}}{\alpha_{21}} \Rightarrow \frac{\alpha_{12}}{\alpha_{22}} > \frac{\alpha_{11}}{\alpha_{21}} \Rightarrow A_3 < 0. \end{aligned}\right\} \quad \ldots(13)$$

Thus $A_1$, $A_2$, $A_3$ or $B_1$, $B_2$, $B_3$ can have the signs

$$+++,\ ---,\ +-+,\ +--,\ -++,\ -+-$$

but cannot have the signs

$$++-,\ --+.$$

We are then left with 36 cases, out of which only in four, corresponding to (12), the nzep exists.

## 3. Stability of Equilibrium Positions

The eigenvalues of the community matrix for determining the stability of the equilibrium positions are the roots of

$$\begin{vmatrix} a_1 - \alpha_{11}\bar{P}_1 - \alpha_{12}\bar{P}_2 - \lambda & 0 & -\alpha_{11}\bar{H}_1 & -\alpha_{12}\bar{H}_1 \\ 0 & a_2 - \alpha_{21}\bar{P}_1 - \alpha_{22}\bar{P}_2 - \lambda & -\alpha_{21}\bar{H}_2 & -\alpha_{22}\bar{H}_2 \\ \beta_{11}\bar{P}_1 & \beta_{22}\bar{P}_1 & -b_1 + \beta_{11}\bar{H}_1 + \beta_{12}\bar{H}_2 - \lambda & 0 \\ \beta_{21}\bar{P}_2 & \beta_{22}\bar{P}_2 & 0 & -b_2 + \beta_{21}\bar{H}_1 + \beta_{22}\bar{H}_2 - \lambda \end{vmatrix} = 0. \quad ...(14)$$

For the six positions of equilibrium, this gives

(i) $(\lambda - a_1)(\lambda - a_2)(\lambda + b_1)(\lambda + b_2) = 0$ ...(15)

(ii) $\left(\frac{\lambda}{\alpha_{12}} - A_1\right)\left(\frac{\lambda}{\beta_{12}} + B_1\right)(\lambda^2 + a_2 b_1) = 0$ ...(16)

(iii) $\left(\frac{\lambda}{\alpha_{21}} - A_2\right)\left(\frac{\lambda}{\beta_{21}} + B_2\right)(\lambda^2 + a_1 b_1) = 0$ ...(17)

(iv) $\left(\frac{\lambda}{\alpha_{22}} + A_2\right)\left(\frac{\lambda}{\beta_{22}} - B_1\right)(\lambda^2 + a_2 b_1) = 0$ ...(18)

(v) $\left(\frac{\lambda}{\alpha_{22}} + A_1\right)\left(\frac{\lambda}{\beta_{22}} - B_2\right)(\lambda^2 + a_1 b_2) = 0$ ...(19)

(vi) $\lambda^4 + \lambda^2(\bar{\alpha}_{11}\bar{\beta}_{11} + \bar{\alpha}_{12}\bar{\beta}_{21} + \bar{\alpha}_{22}\bar{\beta}_{22} + \bar{\alpha}_{21}\bar{\beta}_{12})$
$+ (\bar{\alpha}_{11}\bar{\alpha}_{22} - \bar{\alpha}_{12}\bar{\alpha}_{21})(\bar{\beta}_{11}\bar{\beta}_{22} - \bar{\beta}_{12}\bar{\beta}_{21}) = 0$ ...(20)

where

$$\bar{\alpha}_{jk} = \alpha_{jk}\bar{P}_k, \; \bar{\beta}_{jk} = \beta_{jk}\bar{H}_k. \quad ...(21)$$

Position (i) is always unstable.

Position (ii) will be neutral if $A_1 < 0$, $B_1 > 0$ and will be unstable otherwise.

Position (iii) will be neutral if $A_2 < 0$, $B_2 > 0$ and will be unstable otherwise.

Position (iv) will be neutral if $A_2 > 0$, $B_1 < 0$ and will be unstable otherwise.

Position (v) will be neutral if $A_1 > 0$, $B_2 < 0$ and will be unstable otherwise.

Position (vi) will be neutral if $A_3 > 0$, $B_3 > 0$ or $A_3 < 0$, $B_3 < 0$ and will be unstable if $A_3 > 0$, $B_3 < 0$ or $A_3 < 0$, $B_3 > 0$.

This discussion gives the following Table I where a bar over a number denotes neutral equilibrium for the corresponding equilibrium position and the absence of a bar denotes its unstable equilibrium.

TABLE I

| $A_1A_2A_3$ \ $B_1B_2B_3$ | + + + | + − + | − + + | + − − | − + − | − − − |
|---|---|---|---|---|---|---|
| + + + | $1, 2, 3, 4, 5, \bar{6}$ | $1, 2, 3, 4, \bar{5}$ | $1, 2, 3, \bar{4}, 5$ | $1, 2, 3, 4, \bar{5}$ | $1, 2, 3, \bar{4}, 5$ | $1, 2, 3, \bar{4}, \bar{5}, 6$ |
| + − + | $1, 2, \bar{3}, 4, 5$ | $1, 2, 3, 4, \bar{5}$ | $1, 2, \bar{3}, 4, 5$ | $1, 2, 3, 4, \bar{5}$ | $1, 2, \bar{3}, 4, 5$ | $1, 2, 3, 4, \bar{5}$ |
| − + + | $1, \bar{2}, 3, 4, 5$ | $1, \bar{2}, 3, 4, 5$ | $1, 2, 3, \bar{4}, 5$ | $1, \bar{2}, 3, 4, 5$ | $1, 2\ 3, \bar{4}, 5$ | $1, 2, 3, \bar{4}, 5$ |
| + − − | $1, 2, \bar{3}, 4, 5$ | $1, 2, 3, 4, \bar{5}$ | $1, 2, \bar{3}, 4, 5$ | $1\ 2, 3, 4, \bar{5}$ | $1, 2, \bar{3}, 4, 5$ | $1, 2, 3, 4, \bar{5}$ |
| − + − | $1, \bar{2}, 3, 4, 5$ | $1, \bar{2}, 3, 4, 5$ | $1, 2, 3, \bar{4}, 5$ | $1, \bar{2}, 3, 4, 5$ | $1, 2, 3, \bar{4}, 5$ | $1, 2, 3, \bar{4}, 5$ |
| − − − | $1, \bar{2}, \bar{3}, 4, 5, 6$ | $1, \bar{2}, 3, 4, 5$ | $1, 2, \bar{3}, 4, 5$ | $1, \bar{2}, 3, 4, 5$ | $1, 2, \bar{3}, 4, 5$ | $1, 2, 3, 4, 5, \bar{6}$ |

Thus out of 36 cases, positions (ii), (iii), (iv), (v) are in neutral equilibrium in 9 cases each and position (vi) is in neutral equilibrium in 2 cases. There are 2 cases in which two possible positions can be of neutral equilibrium.

Thus in 34 cases, the ultimate outcome is independent of the initial conditions and can be predicted from only the knowledge of the signs of $A_1$, $A_2$, $A_3$, $B_1$, $B_2$, $B_3$. Thus e.g.

(a) (+ + +, + + +) or (− − −, − − −) implies that the four species will survive and there will be conservative oscillations about the nzep.

(b) (+ − +, + − +) implies that first predator species and second prey species will die out, the second predator species and the first prey species will survive and for these two, there will be conservative oscillation about the value $a_1/\alpha_{12}$ for the predator population and the value $b_2/\beta_{21}$ for the prey population. Similar behaviour will occur in 31 other cases.

(c) (+ + +, − − −) implies that either, $H_2$, $P_1$ will die out and there will be conservative oscillation about $\bar{H}_1$, $\bar{P}_2$ or $H_1$, $P_2$ will die out and there will be conservative oscillations about $\bar{H}_2$, $\bar{P}_1$. Similar behaviour occurs in the case (− − −, + + +).

## 4. NUMERICAL ILLUSTRATIONS

We have carried out extensive numerical integrations and these of course confirm the results obtained theoretically above. We give some typical cases below.

*Case I*

$$\left.\begin{array}{l} a_1 = a_2 = 3;\ \alpha_{11} = \alpha_{22} = 2;\ \alpha_{11} = \alpha_{21} = 1 \\ b_1 = 4,\ b_2 = 2,\ \beta_{11} = 3,\ \beta_{12} = \beta_{21} = \beta_{22} = 1 \end{array}\right\} \quad \ldots(22)$$

$$H_1(0) = 1.25,\ H_2(0) = 0.75,\ P_1(0) = 1.25,\ P_2(0) = 0.75. \qquad ...(23)$$

Here $$\bar{H}_1 = \bar{H}_2 = \bar{P}_1 = \bar{P}_2 = 1,\ A_1, A_2, A_3, B_1, B_2, B_3 > 0. \qquad ...(24)$$

The nzep exists and is in neutral equilibrium

$$\lambda^4 + 10\lambda^2 + 6\lambda = 0 \text{ or } \lambda^2 = -5 \pm \sqrt{19}. \qquad ...(25)$$

There are two components with periods $2\pi/\sqrt{5 - \sqrt{19}}$ and $2\pi/\sqrt{5 - \sqrt{19}}$. Figures 1 and 2 show the conservative oscillations of $H_1$, $H_2$ and $P_1$, $P_2$ about the equilibrium populations. Figures 3, 4, 5, 6 show the projection of the trajectory in the four-dimensional space on the two-dimensional $H_1 - H_2$, $P_1 - P_2$, $H_1 - P_1$, $H_2 - P_2$ subspace of the $H_1 - H_2 - P_1 - P_2$ phase space. Each of these intersects itself while the original trajectory in four-dimensional space does not. At a point of intersection in the $H_1 - H_2$ subspace, $H_1$, $H_2$ have the same values, while $P_1$, $P_2$ have different values.

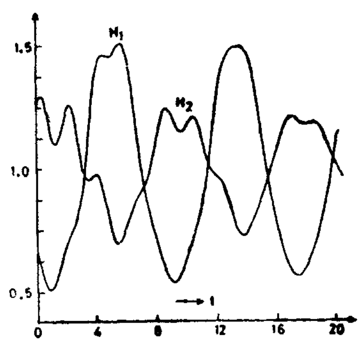


FIG. 1.

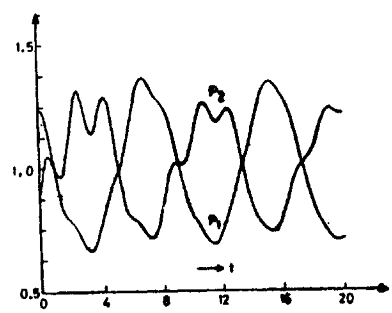


FIG. 2

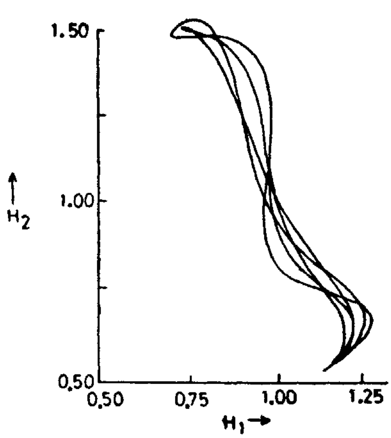


FIG. 3.

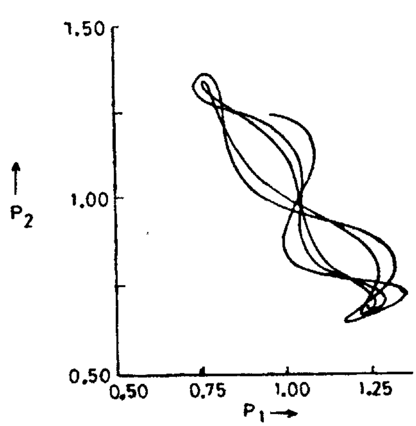


FIG. 4.

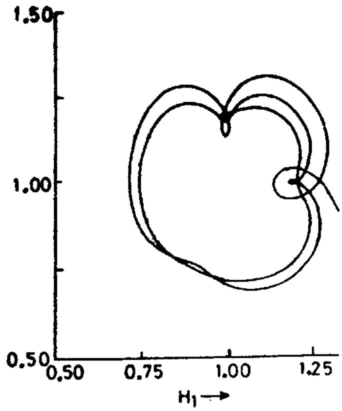


FIG. 5.

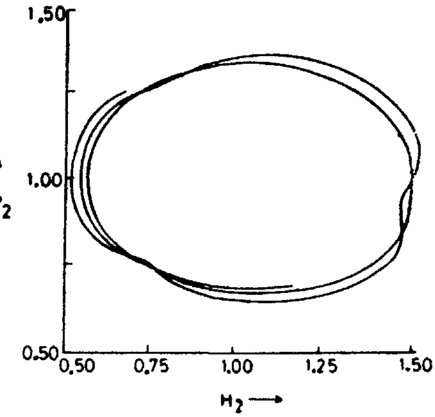


FIG. 6.

*Case II*

$$\left.\begin{array}{llllll} a_1 = 3, & a_2 = 3, & \alpha_{11} = 1, & \alpha_{12} = 2, & \alpha_{21} = 2, & \alpha_{22} = 1 \\ b_1 = 4, & b_2 = 2, & \beta_{11} = 3, & \beta_{12} = 1, & \beta_{21} = 1, & \beta_{22} = 1 \end{array}\right\} \quad \ldots(26)$$

$$\bar{H}_1 = \bar{H}_2 = \bar{P}_1 = \bar{P}_2 = 1, \quad A_1, A_2, A_3 < 0, \quad B_1B_2B_3 > 0. \quad \ldots(27)$$

The nzep exists but is unstable. In this case either $P_1$, $H_1$ or $P_2$, $H_2$ die out.

Figures 7 and 8 refer to the initial conditions

$$H_1(0) = 1.25, H_2(0) = 0.75, P_1(0) = 1.25, P_2(0) = 0.75 \quad \ldots(28)$$

and in this case $H_2P_2$ die out.

*Case III*

$$\left.\begin{array}{llllll} a_1 = 3, & a_3 = 3, & \alpha_{11} = 2, & \alpha_{12} = 1. & \alpha_{21} = 1, & \alpha_{22} = 2 \\ b_1 = 4, & b_2 = 2, & \beta_{11} = 1.5, & \beta_{12} = 1, & \beta_{21} = 1, & \beta_{22} = 2 \end{array}\right\} \quad \ldots(29)$$

$$A_1 > 0, A_2 > 0, A_3 > 0, B_1 > 0, B_2 < 0, B_3 > 0. \quad \ldots(30)$$

Figures 9 and 10 for initial conditions (28) show that $H_2$, $P_1$ die out.

## 5. General Case of $N$ Predator Species and $n$ Prey Species

The number of equilibrium positions in which $r$ predator and $r$ prey species have died out is $n_{c_r} \times n_{c_r}$, so that the total number of equilibrium positions is

$$(n_{c_0})^2 + (n_{c_1})^2 + \ldots + (n_{c_n})^2 = 2n_{c_n} = \frac{\underline{|2n}}{\underline{|n}\,\underline{|n}}\,. \quad \ldots(31)$$

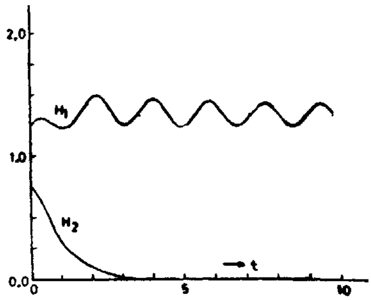


FIG. 7.

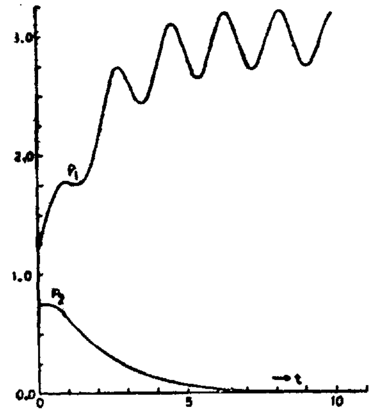


FIG. 8

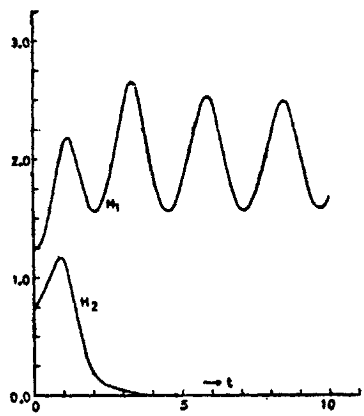


FIG. 9.

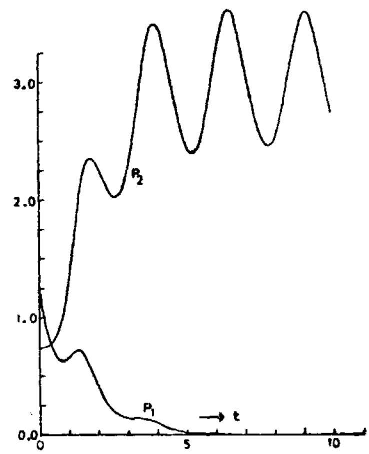


FIG. 10.

For the existence of nzep, we require that

(i) $A_1, A_2, \ldots, A_n, A$ have the same sign

(ii) $B_1, B_2, \ldots, B_n, B$ have the same sign,

where

$$A = \begin{vmatrix} \alpha_{11}\alpha_{12} \ldots \alpha_{1n} \\ \alpha_{21}\alpha_{22} \ldots \alpha_{2n} \\ \cdots\cdots\cdots\cdots \\ a_{n1}\alpha_{n2} \ldots \alpha_{nn} \end{vmatrix}, \quad B = \begin{vmatrix} \beta_{11}\beta_{12} \ldots \beta_{1n} \\ \beta_{21}\beta_{22} \ldots \beta_{2n} \\ \cdots\cdots\cdots\cdots \\ \beta_{n1}\beta_{n2} \ldots \beta_{nn} \end{vmatrix} \quad \ldots(32)$$

and $A_i$ and $B_i$ are obtained respectively from $A$ and $B$ by replacing the $i$th column of $A$ by $a_1, a_2, \ldots, a_n$ and the $i$th column of $B$ by $b_1, b_2, \ldots, b_n$. It can easily be shown that if $A_1, A_2, \ldots, A_n$ are all positive (negative), then $A$ is also positive (negative). Similarly if $B_1, B_2, \ldots, B_n$ are all positive (negative), then $B$ is also positive (negative). Thus the following sign combinations are ruled out

$$+ + + \ldots + -, - - - - - \ldots - + \qquad \ldots(33)$$

so that the total number of cases to be considered is

$(2^{n+1} - 2)^2 = 4(2^n - 1)^2$. Out of these

(i) in two cases viz $(+ + \ldots +, + + \ldots +), - - \ldots - -, - - \ldots - -)$ the nzep exists and is in neutral equilibrium so that in these two cases, all the species survive and there are conservative oscillations about this position.

(ii) In two cases viz $(+ + \ldots + +, - - \ldots - -), (- - \ldots - -, + + - \ldots + +)$, the nzep exists but in unstable. One prey species and one predator species will die out. As to which one will die out will depend in the initial conditions.

(iii) In the remaining $4(2^{2n} - 2^{n+1})$ cases, the nzep does not exist, and one of $({}^nc_1)^2 + \ldots + ({}^nc_{n-1})^2$ equilibrium positions should be in neutral equilibrium and which one it will be depends on model parameters.

The community matrix is given by

$$\begin{bmatrix} a_1 - \sum_{j=1}^{n} \alpha_{1j}\bar{P}_j & 0 & \cdots & 0 & \vdots \\ 0 & a_2 - \sum_{j=1}^{n} \alpha_{2j}\bar{P}_j & \cdots & 0 & \vdots \\ \cdots & \cdots & \cdots & \cdots & \vdots \\ 0 & 0 & \cdots & a_n - \sum_{j=1}^{n} \alpha_{nj}\bar{P}_j & \vdots \\ \cdots & \cdots & \cdots & \cdots & \vdots \\ \beta_{11}\bar{P}_1 & \beta_{12}\bar{P}_1 & \cdots & \beta_{1n}\bar{P}_1 & \vdots \\ \beta_{21}\bar{P}_1 & \beta_{22}\bar{P}_2 & \cdots & \beta_{2n}\bar{P}_2 & \vdots \\ \cdots & \cdots & \cdots & \cdots & \vdots \\ \beta_{n1}\bar{P}_n & \beta_{n2}\bar{P}_n & \cdots & \beta_{nn}\bar{P}_n & \vdots \end{bmatrix}$$

(equation continued on p. 1308)

$$
\left.\begin{array}{cccc}
-\alpha_{11}\bar{H}_1 & -\alpha_{12}\bar{H}_1 & \cdots & -\alpha_{1n}\bar{H}_1 \\
-\alpha_{21}\bar{H}_2 & -\alpha_{22}\bar{H}_2 & \cdots & -\alpha_{2n}\bar{H}_2 \\
\cdots & \cdots & \cdots & \cdots \\
-\alpha_{n1}\bar{H}_1 & -\alpha_{n2}\bar{H}_2 & \cdots & -\alpha_{nn}\bar{H}_n \\
\cdots & \cdots & \cdots & \cdots \\
-b_1+\sum\limits_{j=1}^{n}\beta_{1j}\bar{H}_j & 0 & \cdots & 0 \\
0 & -b_2+\sum\limits_{j=1}^{n}\beta_{2j}\bar{H}_j \cdots & & 0 \\
0 & 0 & \cdots & \cdots\, b_n+\sum\limits_{j=1}^{n}\beta_{nj}\bar{H}_j
\end{array}\right] \qquad \ldots(34)
$$

For the non-zero equilibrium position, all the diagonal elements will be zero and the equilibrium will be either neutral or unstable. This case has been discussed by May (1971, 1973).

In the case of nzep being unstable or its not existing, one pair of species will die out. Let us find the condition that the pair which dies out is $H_1$, $P_1$. In this case all the summations in the above matrix are from $j = 2$ to $n$, and the last $n$ elements of the first row and the first $n$ elements of the $(n + 1)$th row vanish. The eigenvalues are given by

$$\left(a_1 - \sum_{j=2}^{n} \alpha_{1j}\bar{P}_j - \lambda\right)\left(-b_1 + \sum_{j=2}^{n} \beta_{1j}\bar{H}_j - \lambda\right)\phi(\lambda) = 0 \qquad \ldots(35)$$

where $\phi(\lambda) = 0$ is the secular equation for the species $H_2, \ldots, H_n, P_2, P_3, \ldots P_n$. This will give roots $\lambda_1$, $\lambda_2$ where

$$a_1 - \sum_{j=2}^{n} \alpha_{1j}\bar{P}_j = \lambda_1, \; -b_1 + \sum_{j=2}^{n} \beta_{1j}\bar{H}_j = \lambda_2 \qquad \ldots(36)$$

and the roots of $\phi(\lambda) = 0$. Now $\bar{P}_2, \bar{P}_3, \ldots, \bar{P}_n; \bar{H}_2, \bar{H}_3, \ldots, \bar{H}_n$ satisfy the equations

$$a_i - \sum_{j=2}^{n} \alpha_{ij}\bar{P}_j = 0, \; -b_i + \sum_{j=2}^{n} \beta_{ij}\bar{H}_j = 0, \; i = 2, 3, \ldots\ldots, n. \qquad \ldots(37)$$

Eliminating $\bar{P}_2, \bar{P}_3, \ldots, \bar{P}_n, \bar{H}_2, \bar{H}_3, \ldots, \bar{H}_n$, we get

$$\begin{vmatrix} a_1 - \lambda_1 & \alpha_{12} & \cdots & \alpha_{1n} \\ a_2 & \alpha_{22} & \cdots & \alpha_{2n} \\ \cdots & \cdots & \cdots & \cdots \\ a_n & \alpha_{n2} & \cdots & \alpha_{nn} \end{vmatrix} = 0 \qquad \begin{vmatrix} b_1 + \lambda_2 & \beta_{12} & \cdots & \beta_{1n} \\ b_2 & \beta_{22} & \cdots & \beta_{2n} \\ \cdots & \cdots & \cdots & \cdots \\ b_n & \beta_{n2} & \cdots & \beta_{nn} \end{vmatrix} = 0 \qquad \ldots(38)$$

or $$A_1 - \lambda_1 A_{11} = 0,\ B_1 + \lambda_2 B_{11} = 0 \qquad \text{...(39)}$$

where $A_{11}$, $B_{11}$ are respectively the cofactors of $\alpha_{11}$, $\beta_{11}$ in $A$ and $B$. Therefore if $P_1$, $H_1$ are to vanish and the other species have to survive and give conservative oscillations about the equilibrium position, thus

$$\frac{A_1}{A_{11}} < 0,\ \frac{B_1}{B_{11}} > 0 \qquad \text{...(40)}$$

and all the roots of $\phi(\lambda) = 0$ should be purely imaginary.

In the same way, to find the condition that $P_1$, $H_1$, $P_2$, $H_2$ die out and the remaining species survive and perform conservative oscillation, we shall have

$$\left.\begin{array}{l} a_1 - \sum\limits_{j=3}^{n} \alpha_{1j}\bar{P}_j - \lambda_3 = 0,\ \ a_2 - \sum\limits_{j=3}^{n} \alpha_{2j}\bar{P}_j - \lambda_4 = 0 \\ -\, b_1 + \sum\limits_{j=3}^{n} \beta_{1j}\bar{H}_j - \lambda_5 = 0,\ -\, b_2 + \sum\limits_{j=3}^{n} \beta_{2j}\bar{H}_j - \lambda_6 = 0 \end{array}\right] \qquad \text{...(41)}$$

where

$$a_i - \sum_{j=3}^{n} \alpha_{ij}\bar{P}_j = 0,\ -\, b_i + \sum_{j=3}^{n} \beta_{ij}\bar{H}_j = 0. \qquad \text{...(42)}$$

From (41) and (42) we get

$$\begin{vmatrix} a_1 - \lambda_3 & \alpha_{13} & \cdots & \alpha_{1n} \\ a_3 & \alpha_{33} & \cdots & \alpha_{3n} \\ \cdots & \cdots & \cdots & \cdots \\ a_n & \alpha_{n3} & \cdots & \alpha_{nn} \end{vmatrix} = 0, \quad \begin{vmatrix} a_2 - \lambda_4 & \alpha_{23} & \cdots & \alpha_{2n} \\ a_3 & \alpha_{33} & \cdots & \alpha_{3n} \\ \cdots & \cdots & \cdots & \cdots \\ a_n & \alpha_{n3} & \cdots & \alpha_{nn} \end{vmatrix}$$

$$\begin{vmatrix} b_1 + \lambda_5 & \beta_{13} & \cdots & \beta_{1n} \\ b_3 & \beta_{33} & \cdots & \beta_{3n} \\ \cdots & \cdots & \cdots & \cdots \\ b_n & \beta_{n3} & \cdots & \beta_{nn} \end{vmatrix} = 0, \quad \begin{vmatrix} b_2 + \lambda_6 & \beta_{23} & \cdots & \beta_{2n} \\ b_3 & \beta_{33} & \cdots & \beta_{3n} \\ \cdots & \cdots & \cdots & \cdots \\ b_n & \beta_{n3} & \cdots & \beta_{nn} \end{vmatrix} \qquad \text{...(43)}$$

The required conditions are that $\lambda_3$, $\lambda_4$, $\lambda_5$, $\lambda_6$ should be negative and the roots of the secular equation for the species $H_3$, ..., $H_n$, $P_3$, ..., $P_n$ should be purely imaginary.

All these conditions depend on the ecological constraints. However at any stage if the nzep is unstable, then more than one equilibrium position may be in neutral equilibrium and which species will finally survive will also depend on the initial conditions.

## 6. Discussion of Special Pathological Cases

In section 3 we confined ourselves essentially to the cases when each $A_i$ and $B_i$ is either positive or negative and for these cases we made the statement that one predator species and one prey species can die out. However it is possible that some of the $A_i$'s and $B_i$'s may be zero and in these cases either a prey-species or a predator species (and not both) may die out and we may be left with a system with an unequal number of prey and predator species. Such cases are rather unlikely and we have called them pathological. However these must be taken into account when we want to make general statements.

Consider the model

$$\left.\begin{aligned} \frac{dH_1}{dt} &= H_1[3 - P_1 - P_2], \quad \frac{dH_2}{dt} = H_2[5 - P_1 - 2P_2] \\ \frac{dP_1}{dt} &= P_1[-2 + \tfrac{1}{2}H_1 + H_2], \quad \frac{dP_2}{dt} = P_2[-4 + H_1 + 2H_2]. \end{aligned}\right\} \qquad \ldots(44)$$

This has an infinity of non-zero equilibrium positions, viz.

$$\bar{P}_1 = 1, \bar{P}_2 = 2, \ \bar{H}_1 = 4 - 2x, \bar{H}_2 = x, \quad 0 < x < 2. \qquad \ldots(45)$$

Equation (20) gives

$$\lambda^4 + \lambda^2(4x + 10) = 0. \qquad \ldots(46)$$

All the positions are unstable. Atleast one species will disappear

(1) Let the disappearing species be $H_1$, then, we get

$$\left.\begin{aligned} \frac{dH_1}{dt} &= H_2[5 - P_1 - 2P_2], \quad \frac{dP_1}{dt} = P_1[-2 + \tfrac{1}{2}H_1 + H_2], \\ \frac{dP_2}{dt} &= P_2[-4 + H_1 + 2H_2]. \end{aligned}\right\} \qquad \ldots(47)$$

This has an infinity of equilibrium positions

$$\bar{H}_2 = 2, \ \bar{P}_1 = 5 - 2y, P_2 = y, \quad 0 < y < \tfrac{5}{2} \qquad \ldots(48)$$

and the eigenvalues are given by

$$\begin{vmatrix} -\lambda & -2 & -4 \\ 3 - 2y & -\lambda & 0 \\ y & 0 & -\lambda \end{vmatrix} = 0 \text{ or } \lambda(\lambda^2 + 6) = 0. \qquad \ldots(49)$$

The three species (1 prey and 2 predators) can coexist and oscillate with a period $2\pi/\sqrt{6}$ about a position which depends on initial conditions.

Again suppose that $H_2$ disappears, then we get

$$\frac{dH_1}{dt} = H_1(3 - P_1 - P_2), \frac{dP_1}{dt} = P_1(-2 + \tfrac{1}{2}H_1), \frac{dP_2}{dt} = P_2(-4 + H_1) \quad \text{...(50)}$$

$$\bar{H}_1 = 4, \ \bar{P}_1 = z, \ \bar{P}_2 = 3 - z, \quad 0 < z < 3 \quad \text{...(51)}$$

$$\lambda(\lambda^2 - 2z + 12) = 0 \quad \text{...(52)}$$

so that the three species (first prey and two predator) can still coexist and oscillate about a position depending on initial conditions.

It is easily seen that for our model, one predator and 2 prey species cannot survive. However we can have other models in which this can be possible e.g. for the model

$$\frac{dH_1}{dt} = H_1(3 - P_1), \ \frac{dH_2}{dt} = H_2(3 - P_1), \ \frac{dP_1}{dt} = P_1(2 - H_1 - H_2) \quad \text{...(53)}$$

there is an infinity of equilibrium position with

$$\bar{P}_1 = 3, \ \bar{H}_1 + \bar{H}_2 = 2 \quad \text{...(54)}$$

for which

$$\lambda(\lambda^2 + 3\bar{H}_2 + \bar{H}_1) = 0 \quad \text{...(55)}$$

so that two prey and one predator species can coexist and perform conservative oscillation about position depending on initial conditions.

Thus predator-prey models with unequal number of prey and predator species can coexist and perform conservative oscillations. However such models require severe restriction on model parameters and are likely to be rare.

## REFERENCES

Lotka, A. J. (1925). Elements of Physical Biology. Williams and Wilkins, Baltimore, New York (reissued by Dover in 1956).

May, R. M. (1971). Stability in multispecies community models. *Math. Biosci.*, 12, 59–75.

——————— (1973). Stability and Complexity in Model Ecosystems. Princeton University Press, Princeton.