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HARVESTING COMPETING POPULATIONS

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This article is a brief report on work done by A. J. Reading in 1975–76 as part of an undergraduate research project in the mathematics department of the University of Bristol. It is an extension of the work of Brauer and Sánchez [1] on population dynamics when one species is harvested at a constant rate.

We consider a system of two competing species, represented by the following deterministic differential equation system:

$$(1)\qquad \begin{aligned} dx/dt &= x(\lambda - ax - by) - E, \\ dy/dt &= y(\mu - cx - dy) - F. \end{aligned}$$

Here x, y are the sizes or densities of the two populations, λ, μ, a, b, c, d are positive constants representing the growth and competition coefficients, and E, F are non-negative constants representing the number of members of each population harvested (i.e., removed) per unit time. We assume that the harvesting does not change the values of the vital coefficients a, b, c, d, λ, μ.

If there is no harvesting, i.e., $E = F = 0$, then the two species can coexist in stable equilibrium only if

$$(2)\qquad a\mu - c\lambda > 0 \text{ and } d\lambda - b\mu > 0;$$

we shall assume throughout that (2) is satisfied. The zero isoclines Z_x, Z_y in the phase plane (defined as the curves along which dx/dt, dy/dt respectively vanish) for the case $E = F = 0$ are as shown in Figure 1.

If $E > 0$, Z_x becomes a hyperbola whose asymptotes are the y-axis and the line (shown dotted in Fig. 2) corresponding to the unharvested Z_x; similarly Z_y becomes a hyperbola if the y population is harvested. If E, F are fairly small, the hyperbolae lie close to their asymptotes and intersect each other four times, as shown in Figure 2. Three of those intersections correspond to unstable equilibria, and one, marked S in Figure 2, gives a stable equilibrium point.

A natural question to ask is the following: is it possible to use harvesting to maintain the populations at predetermined sizes? in other words, given x_0, y_0, do there exist $E, F \geqq 0$ such that (x_0, y_0) is a stable equilibrium point of (1)? This question is readily answered by first read-

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ing off the required values of E, F from (1), and then substituting them into the condition

$$(a - E/x_0^2)(d - F/y_0^2) > bc \tag{3}$$

for stability of the equilibrium point (x_0, y_0) (obtained fom the usual linearised stability analysis). Thus one can find a region in the xy plane of population sizes which can be maintained in stable equilibrium by a suitable constant-rate harvesting policy; it turns out to be bounded by a hyperbola, and is easily drawn when values of a, b, c, d, λ, μ are known.

As the harvesting rate E is increased, the vertex of Z_x in Figure 2 moves downwards; if $E > \lambda^2/4a$ no part of Z_x lies in the first quadrant, and therefore $dx/dt < 0$ for all x, y and the x population is bound to die out. Similarly if $F > \mu^2/4c$ the y population will die out. But if

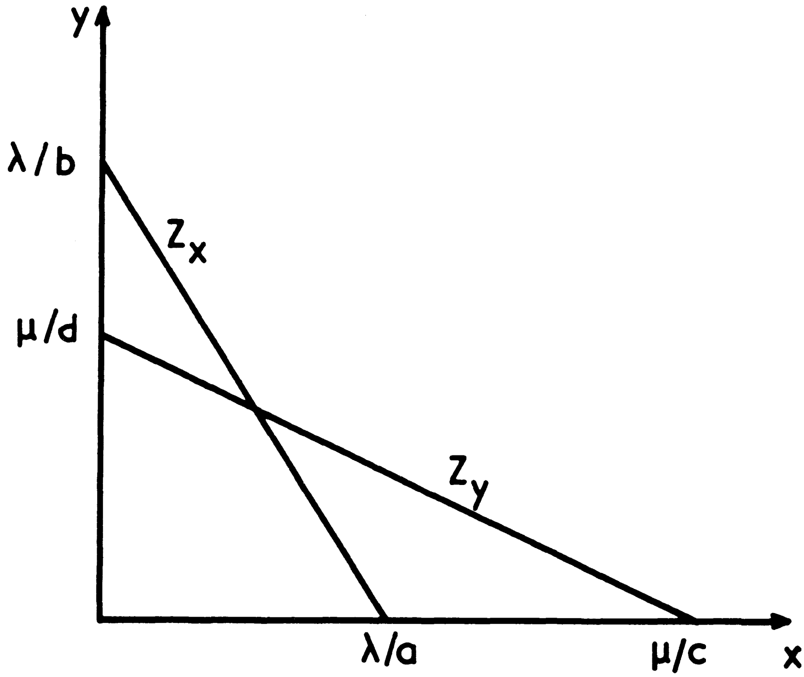

Figure 1
The unharvested phase plane. Z_x, Z_y are the isoclines for zero growth of x, y.

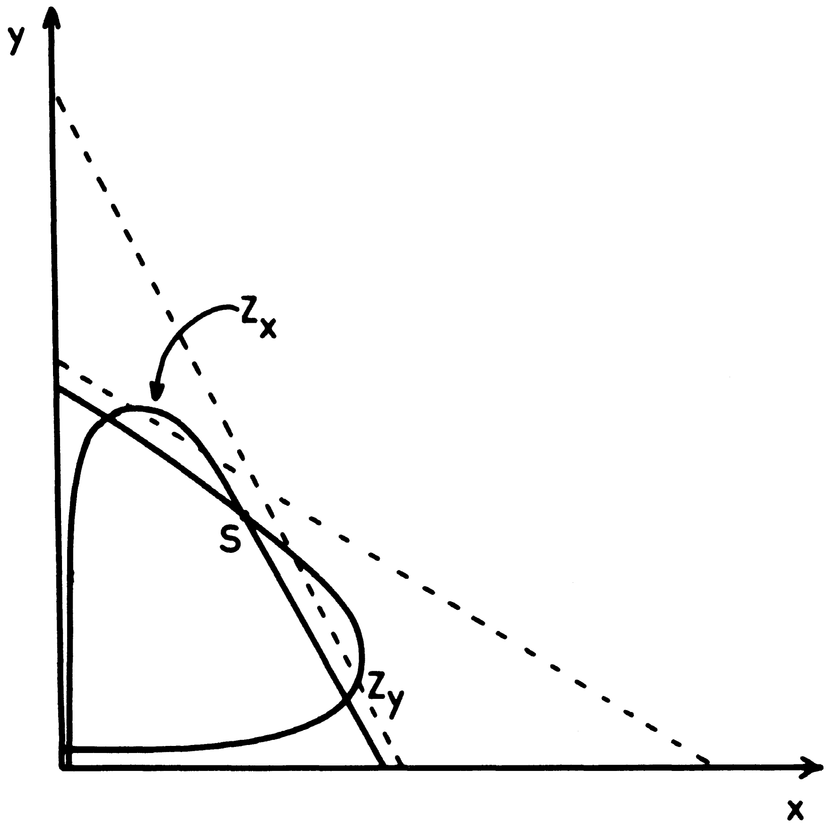

Figure 2
The phase plane with fairly small harvesting. S is the stable two-species equilibrium point.

$E < \lambda^2/4a$ and $F < \mu^2/4c$ the behaviour is more complicated.

If E, F lie in region I of the EF plane (see Fig. 3), corresponding to the conditions of Figure 2, then there are four two-species equilibria, one of which is stable. The cusp-shaped boundary of I in Figure 3 corresponds to values of E and F such that the hyperbolae Z_x, Z_y of Figure 2 touch, while intersecting at two other points. In region II Z_x and Z_y intersect twice, giving two equilibria, both of which are unstable, so that one species must die out. The smooth boundary of II corresponds to E, F such that Z_x touches Z_y without any other intersections; region III and region II both correspond to harvesting rates which result in the extinction of one of the populations; which one survives depends on

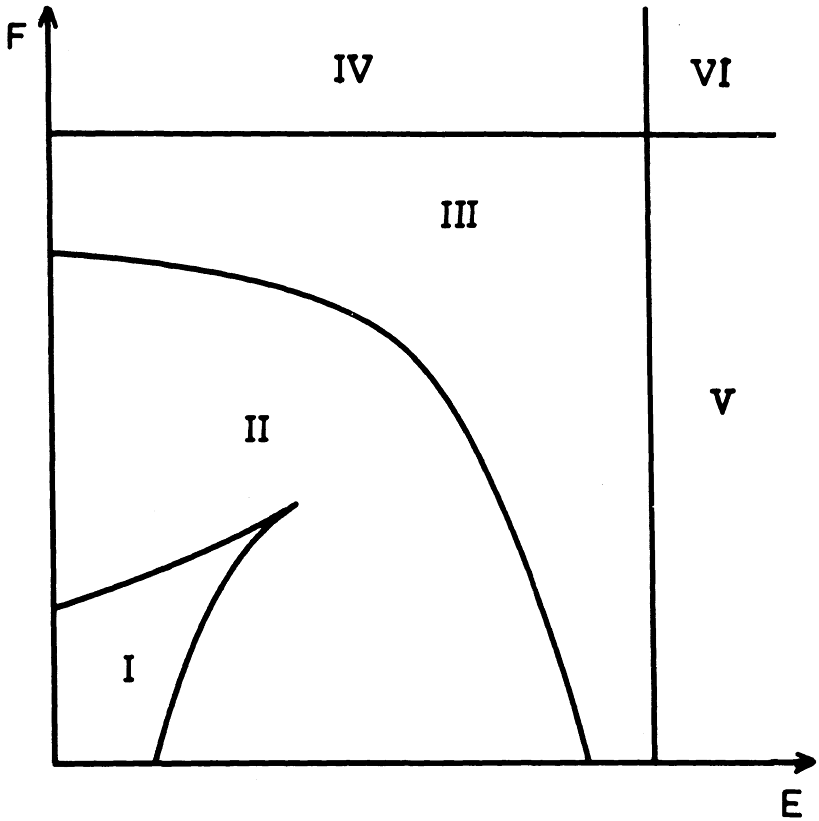

Figure 3
The harvest-rate plane, divided into regions according to the number of equilibria of the system.

the initial conditions. In region IV the y population is bound to die out, in region V the x population is bound to die out, and in region VI both populations die out.

If it is assumed that when one population dies out then one continues to harvest the other at the same rate, then there are single-species equilibria in addition to those discussed above, at the points in the xy plane where Z_x, Z_y cut the axes. The one on each axis which is closer to the origin is unstable; the others are stable. It is a nice exercise to draw the regions of attraction of the stable equilibria, and see how they change and coalesce as E and F are varied.

Although the pictures have been drawn, and calculations performed, assuming the specific model (1), the behaviour will be essentially the same for any model of a similar character. Yodzis [5] has discussed more general models and their implications for species diversity and stability of complex ecosystems.

Finally, it may be noted that the boundaries between regions I, II, and III resemble a plane section through the hyperbolic umbilic catastrophe set (see, e.g., [4]); in particular, the boundary of I is a cusp. We therefore expect the usual hysteresis or delay-jump behaviour when E and F are changed so that (E, F) passes across I. (see, e.g., [3]). However, catastrophe theory is not immediately applicable to this system, because the differential equations (1) are not derivable from a potential function; the proper mathematical setting for Figure 3 is the theory of bifurcations of vector fields [2].

References

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