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ON THE STABILITY OF ONE-PREDATOR TWO-PREY SYSTEMS

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1. Introduction. The MacArthur-Rosenzweig "graphical criterion" of stability says, loosely speaking, that if, in a predator-prey system, the interior equilibrium point lies on the decreasing branch of the prey's zero-isocline, then it is asymptotically stable; it if lies on the increasing branch (in the prey-predator phase plane) then it *may be* unstable (see [**7, 3**]; in case the predator's zero-isocline is a vertical straight line i.e., there is no intraspecific competition in the predator species, it *is* unstable). Freedman and the author have generalized this criterion to the three-dimensional case when there are two predator species competing for a single prey species [**1, 2**]. We have shown that if there is no direct interspecific competition between the predator species and the derivative with respect to the prey quantity of the specific growth rate function of the prey is negative at the interior equilibrium, then this equilibrium is asymptotically stable. In [**2**] we have shown by some drawings the intuitive geometric meaning of the MacArthur-Rosenzweig criterion, namely, that if the condition is fulfilled, and the system is driven out of the equilibrium in an easily controllable way, then the dynamics drives it closer to the equilibrium.

In the present paper we are going to show that the MacArthur-Rosenzweig criterion does not generalize to three-dimensional systems with two competing prey species in the general case. We are giving sufficient conditions for the asymptotic stability of an interior equilibrium. The conditions might be considered more or less known, at least in case the specific growth rates are linear functions, i.e., in case we have a Lotka-Volterra system (see Hutson and Vickers [**5**] and the references therein and Svirezhev, Logofet [**8**]). The relation of these conditions to some concerning permanent coexistence will also be pointed out (cf: [**5**] and see also [**4, 6**]). We shall show the special case in which the MacArthur-Rosenzweig criterion can be generalized.

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2. A sufficient criterion of stability. Let $R_+ = [0, \infty)$, and let $x_1(t), x_2(t), y(t)$ denote the quantities of prey 1, prey 2 and the predator at time t, respectively; the specific growth rate functions of prey i, $i = 1, 2$, and of the predator will be denoted by $F_i : \mathbf{R}^4_+ \mapsto \mathbf{R}$, $G : \mathbf{R}^3_+ \mapsto \mathbf{R}$, respectively, and these functions will be assumed to belong to the C^1 class. The general Kolmogorov-system governing the dynamics of this three-species system is

$$\begin{aligned} \frac{dx_1}{dt} &= x_1 F_1(x_1, x_2, y, K_1) \\ \frac{dx_2}{dt} &= x_2 F_2(x_1, x_2, y, K_2) \\ \frac{dy}{dt} &= yG(x_1, x_2, y), \end{aligned} \tag{2.1}$$

where

$$F_i(0, 0, 0, K_i) > 0, \quad K_i > 0, \tag{2.2}$$

$$\begin{gathered} (x_1 - K_1)F_1(x_1, 0, 0, K_1) < 0, \quad (x_2 - K_2)F_2(0, x_2, 0, K_2) < 0, \\ x_1 \neq K_1, \quad x_2 \neq K_2, \end{gathered} \tag{2.3}$$

$$F_{ix_k}(x_1, x_2, y, K_i) \leq 0, \quad F_{iy}(x_1, x_2, y, K_i) < 0, \quad i \neq k \tag{2.4}$$

$$\begin{gathered} G(0, 0, y) < 0, \quad G_{x_i}(x_1, x_2, y) > 0, \quad G_y(x_1, x_2, y) \leq 0, \\ i = 1, 2, \quad k = 1, 2. \end{gathered} \tag{2.5}$$

These are natural conditions expressing that if the quantities are small then: the prey species may grow (2.2); the i-th prey has carrying capacity $K_i > 0$, and it grows in the absence of competitor and predator up to this value (2.3); there *may be* interspecific competition between the two prey species, and there *is* predation (2.4); the predator dies out in absence of prey, both preys are beneficial to the predator; and there *may be* intraspecific competition in the predator species (2.5). We assume also that the system has an equilibrium point $E = (x_1^0, x_2^0, y^0)$ in the interior of the positive octant of x_1, x_2, y space, i.e.,

$$\begin{gathered} \exists x_1^0 > 0, \ x_2^0 > 0, \ y^0 > 0 \text{ such that} \\ F_1(x_1^0, x_2^0, y^0, K_1) = F_2(x_1^0, x_2^0, y^0, K_2) = G(x_1^0, x_2^0, y^0) = 0. \end{gathered} \tag{2.6}$$

THEOREM 2.1. *Assume that, at E,*

$$F_{1x_1} \leq 0, \quad F_{2x_2} \leq 0, \quad F_{1x_1}^2 + F_{2x_2}^2 > 0, \tag{2.7}$$

$$F_{1x_1}F_{2x_2} - F_{1x_2}F_{2x_1} \geq 0, \tag{2.8}$$

$$F_{1y}F_{2x_2} - F_{1x_2}F_{2y} \geq 0, \quad F_{1x_1}F_{2y} - F_{1y}F_{2x_1} \geq 0, \tag{2.9}$$

and at least one of the inequalities (2.9) *is strict; then E is asymptotically stable.*

PROOF. The proof is a routine application of the Routh-Hurwitz criterion. We present it for the sake of reference in the next section. The characteristic polynomial of the linearized system at E is (the values of all the functions are to be taken at $E = (x_1^0, x_2^2, y^0)$):

(2.10)

$$\begin{aligned} D(\lambda) =& \lambda^3 - \lambda^2(x_1^0F_{1x_1} + x_2^0F_{2x_2} + y^0G_y) \\ &+ \lambda[x_1^0x_2^0(F_{1x_1}F_{2x_2} - F_{1x_2}F_{2x_1}) \\ &\quad + x_1^0y^0(F_{1x_1}G_y - F_{1y}G_{x_1}) + x_2^0y^0(F_{2x_2}G_y - F_{2y}G_{x_2})] \\ &+ x_1^0x_2^0y^0[G_{x_1}(F_{1y}F_{2x_2} - F_{1x_2}F_{2y}) + G_{x_2}(F_{1x_1}F_{2y} - F_{1y}F_{2x_1}) \\ &\qquad - G_y(F_{1x_1}F_{2x_2} - F_{1x_2}F_{2x_1})]. \end{aligned}$$

This polynomial is stable if and only if all the coefficients are positive and the Routh-Hurwitz criterion holds, i.e.,

(2.11)

$$\begin{aligned} &x_1^0x_2^0y^0(F_{1x_2}F_{2y}G_{x_1} + F_{1y}F_{2x_1}G_{x_2} - 2F_{1x_1}F_{2x_2}G_y) \\ &- ({x_1^0}^2x_2^0F_{1x_1} + x_1^0{x_2^0}^2F_{2x_2})(F_{1x_1}F_{2x_2} - F_{1x_2}F_{2x_1}) \\ &- {x_1^0}^2y^0F_{1x_1}(F_{1x_1}G_y - F_{1y}G_{x_1}) - {x_2^0}^2y^0F_{2x_2}(F_{2x_2}G_y - F_{2y}G_{x_2}) > 0. \end{aligned}$$

(2.7) and (2.5) imply that the coefficient of λ^2 is positive, (2.8), (2.4) and (2.5) imply that the coefficient of λ is positive, (2.4), (2.5), (2.7), (2.8) and (2.9) imply that the constant term is positive. These conditions imply also that (2.11) holds: at least one of the last two terms is strictly positive, while the rest of the terms are nonnegative. This proves the theorem. □

3. The intuitive meaning of the stability conditions. Ecologically, condition (2.7) means that we may expect stability if at the equilibrium point the growth rate F_i of the i-th prey is decreasing with the increase of x_i, $i = 1, 2$. This is *the condition corresponding to the MacArthur-Rosenzweig criterion* but, clearly, it is not sufficient now for stability.

(2.8) is a well known condition for two-dimensional competitive systems ensuring the stability of the interior equilibrium representing coexistence. If we write it in the form

$$F_{1x_1}/F_{2x_1} > F_{1x_2}/F_{2x_2}, \tag{3.1}$$

assuming that the denominators are nonzero, then we see that it requires *a stronger intraspecific competition rather than an interspecific one*. It holds true, for instance, if $|F_{ix_i}| > |F_{kx_i}|$, $i \neq k$, $i = 1, 2$, $k = 1, 2$. No wonder that we need this condition also in the three-dimensional case.

Inequalities (2.9) can be written in the form

$$F_{1x_2}/F_{2x_2} \leq F_{1y}/F_{2y} \leq F_{1x_1}/F_{2x_1}, \tag{3.2}$$

provided that the denominators are nonzero. As we see, this requires that the ratio F_{1y}/F_{2y} should be between the two values occurring in (3.1). This, clearly, means that *the predator should not have a strong preference of any of the preys over the other.*

Besides the ecological meaning, the conditions of Theorem 2.1 have a nice geometrical interpretation, too. This enables one to determine the stability by inspection if the graphs of the zero isoclines of the two preys and the predator have been drawn, say, by a computer.

Consider the *cross product* of the gradients of F_1 and F_2 at the equilibrium (all functions are to be taken at $E = (x_1^0, x_2^0, y^0)$):

$$v = \operatorname{grad} F_1 \times \operatorname{grad} F_2 = [F_{1x_2}F_{2y} - F_{1y}F_{2x_2}, F_{1y}F_{2x_1} - F_{1x_1}F_{2y}, \\ F_{1x_1}F_{2x_2} - F_{1x_2}F_{2x_1}].$$

The conditions (2.8)–(2.9) mean that the first two coordinates of this vector should be nonpositive (one of them at least, negative) and the third one nonnegative. Now, the vector v is the tangent vector of the curve of intersection of the surfaces $F_1 = 0$, $F_2 = 0$, and the relative position of these surfaces determine the direction of v (the gradient

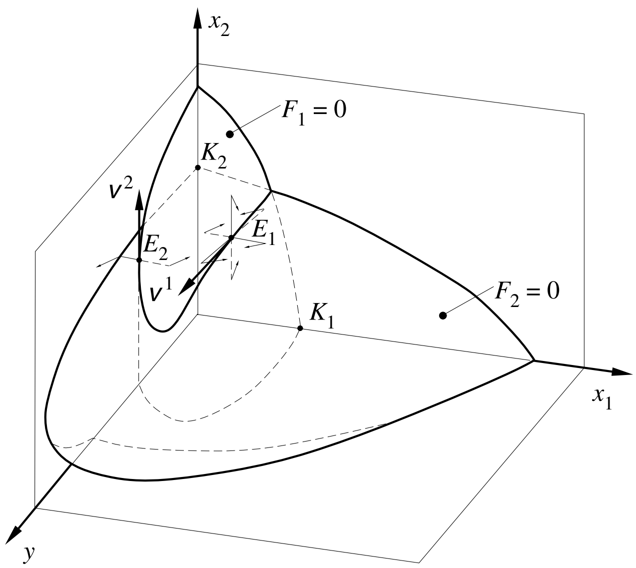

FIGURE 1

points roughly towards the origin since F_i is a decreasing function of x_1, x_2, y at $\dot{E}$). We are showing two generic situations on Figures 1 and 2. On Figure 1 the equilibrium E_1 is stable by inspection. We have shown by the little arrows that if we move out the system from this equilibrium by keeping two of the coordinates fixed and varying only the third one a little, the dynamics tries to drive the system back, closer to E_1. The equilibrium E_2 is, probably, unstable (the conditions imposed upon the signs of the coordinates of the vector v are only sufficient for stability). On Figure 2 the equilibrium E might be unstable (the conditions don't hold). In all these cases the direction of the tangent vectors v^1, v^2 and v can be determined by a careful application of the "right hand rule." In both cases we assumed that the graph of $G = 0$ is (typically) something like in Figure 3.

Note that the constant term in the characteristic polynomial (2.10) is a negative multiple of the scalar product of $\operatorname{grad} G$ with the vector v.

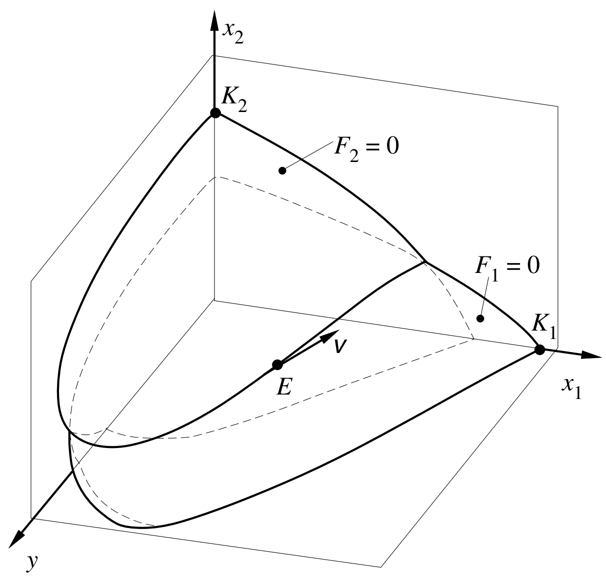

FIGURE 2

Our conditions imply its positivity. If it is negative, i.e., *if* grad G *and* v *form an acute angle, then the equilibrium is unstable.* Note that, in the case shown on Figure 1, the two-dimensional competitive system derived from (2.1) by substituting $y = 0$, has a single asymptotically stable equilibrium in the interior of the positive quadrant of the x_1, x_2 plane. In the case shown in Figure 2, the two-dimensional system is "bistable": it has an unstable equilibrium in the interior, and the equilibria $(x_1, x_2) = (K_1, 0), (x_1, x_2) = (0, K_2)$ are asymptotically stable. We know that if F_1, F_2 and G are linear, i.e., we have a Lotka-Volterra system, then a bistable situation of two competing preys cannot be "stabilized" by a predator (see Hutson, Vickers [**5**]; "stabilized" here means making the system permanently coexistent). We note also that in this Lotka-Volterra case the conditions in Theorem 2.1 imply the conditions of Theorem 3.4 of [**5**], i.e., they imply permanent coexistence provided that *both* $F_{ix_i} < 0$.

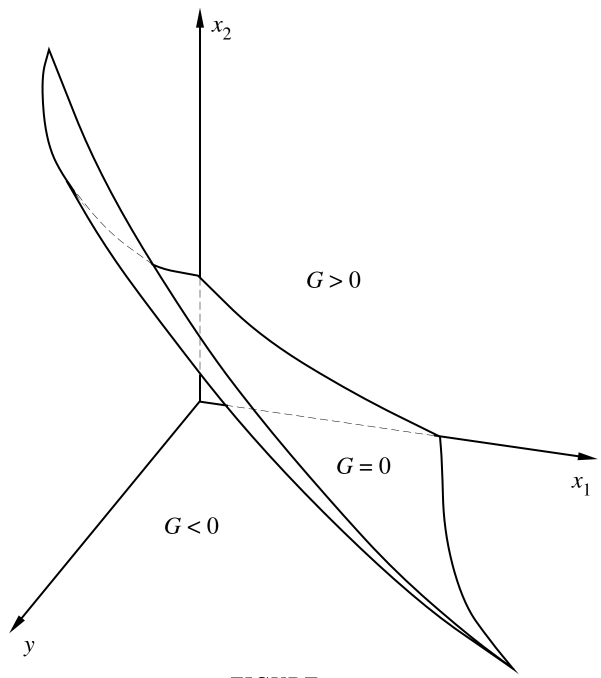

FIGURE 3

4. The neutral case. In [**1, 2**] we have shown that, in a two-predators one-prey system, if there is no direct interspecific competition between the predator species besides consuming the same resource, then the MacArthur-Rosenzweig criterion can be generalized in a natural way. An easy inspection of the conditions (2.7)–(2.9) show that the same is true for one-predator two-prey systems.

Consider a special case of (2.1):

$$\frac{dx_1}{dt} = x_1F_1(x_1, y, K_1), \quad \frac{dx_2}{dt} = x_2F_2(x_2, y, K_2) \tag{4.1}$$
$$\frac{dy}{dt} = yG(x_1, x_2, y)$$

with conditions (2.2)–(2.6) except, of course, that now $F_{ix_k}(x_i, y, K_i) \equiv 0$, $i \neq k$. There holds the following

THEOREM 4.1. *If* (2.7) *holds for system* (4.1) *at* E, *then this equilibrium is asymptotically stable.*

PROOF. This is an immediate corollary of Theorem 2.1. □

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