Appendix C: Stability of the Rosenzweig-MacArthur model with a generalized Holling type functional response.

Stability at infinite enrichment

An alternative model of a closed system with logistically growing prey consists of the following set of two differential equations:

$$\frac{dG}{dt} = e\frac{aR^b}{1+ahR^b}G - mG \tag{C.1}$$

$$\frac{dR}{dt} = r\left(1-\frac{R}{K}\right)R - \frac{aR^b}{1+ahR^b}G \tag{C.2}$$

with all parameters as described in Table 1 and algal carrying capacity K. This is the classical Rosenzweig-MacArthur model with a generalized Holling type functional response. In order to derive a stability criterion at infinite enrichment (analogous to eq. B.9), we first calculate the algal isocline by setting eq. (C.2) to zero and solving for G, which yields

$$G = \frac{r}{a}\left(R^{1-b} - \frac{R^{2-b}}{K} + ahR - \frac{ahR^2}{K}\right). \tag{C.3}$$

Similar to the full model, the algal isocline (eq. C.3) has one local minimum at low algal density and one local maximum if the system is sufficiently enriched. At infinite enrichment ($K \to \infty$) eq. C.3 simplifies to

$$G = \frac{r}{a}\left(R^{1-b} + ahR\right). \tag{C.4}$$

We set the first derivative of eq. C.4 $dG/dR = 0$ and solve for R'

$$R' = \sqrt[b]{\frac{b-1}{ah}}\ . \tag{C.5}$$

R' is also the algal density at which the grazer's clearance rate has a maximum. The second derivative of eq. C.4 is

$$\frac{d^2G}{dR^2} = -\frac{rb(1-b)}{aR^{b+1}}. \tag{C.6}$$

which is positive if b>1 (i.e. the grazer has a type III functional response). Then the algal isocline has a local minimum at R'.

The grazer isocline can be derived by setting eq. C.1 to zero and solving for R, which yields

$$R^* = \sqrt[b]{\frac{m}{a(e-mh)}}. \tag{C.7}$$

The system is stable if $R^* < R'$, i.e. if

$$\sqrt[b]{\frac{m}{a(e-mh)}} < \sqrt[b]{\frac{b-1}{ah}}. \tag{C.8}$$

This inequality is satisfied if

$$\frac{e}{e-mh} < b. \tag{C.9}$$

Note that ineq. C.9 is identical to the stability condition of the full model (eq. B.9), because the Rosenzweig-MacArthur model is closed (i.e., $D = 0$).

A general stability condition derived by Sugie et al. (1997)

Sugie et al. (1997) derived a general, sufficient condition for stability of the model described by eqs. C.1 and C.2. The authors used a Monod type notation for the functional response

$$f(R) = \frac{I_{\max} R^b}{H^b + R^b} \tag{C.10}$$

where H is the half saturation constant of the predator and the maximum ingestion rate $I_{\max}$ was scaled to unity. The latter corresponds to a Holling notation where all rates are scaled to a unit handling time. Translating Sugie et al.'s (1997) stability conditions into the Holling notation yields the following three inequalities:

$$e - mh > 0\,, \tag{C.11}$$

$$K > R^* = \sqrt[b]{\frac{m}{a(e - mh)}}\,, \tag{C.12}$$

and

$$[bmh - (b-2)e]R^* \geq [bmh - (b-1)e]K\,. \tag{C.13}$$

Conditions C.11 and C.12 guarantee feasibility of an interior equilibrium with $R^* > 0$ and $G^* > 0$. Condition C.13 can be rearranged to yield

$$[b(e - mh) - 2e]R^* \leq [b(e - mh) - e]K\,. \tag{C.14}$$

Sugie et al. did not analyze these stability conditions further. Insight into the influence of b on stability can, however, be gained by distinguishing three cases (assuming that condition C.11 holds).

<u>Case 1:</u> $b > 2\dfrac{e}{e - mh}$

In this case the term in brackets on the left hand side of ineq. C.14 is positive and the stability condition can be rearranged to

$$R^* \leq \frac{b(e - mh) - e}{b(e - mh) - 2e}K\,. \tag{C.15a}$$

Because $b > 2e/(e - mh)$ is assumed in case 1, the ratio on the right hand side is > 1. Condition C.15a is thus a weaker condition than C.12 and the system is stable if an interior equilibrium exists.

Case 2: $\frac{e}{e-mh} < b < 2\frac{e}{e-mh}$

In this case the term in brackets on the left hand side of ineq. C.14 is negative and the stability condition can be rearranged to

$$R^* \geq \frac{b(e-mh)-e}{b(e-mh)-2e}K\,. \tag{C.15b}$$

Condition $b > e/(e-mh)$ implies that the numerator in ineq. C.15b is positive. Thus, the right hand side of ineq. C.15b is negative and the system is stable if an interior equilibrium exists.

Case 3: $b < \frac{e}{e-mh}$

In this case stability condition C.15b applies, too, but now the ratio on the right hand side is positive (and smaller than 1). Substituting the right hand side of eq. C.12 into C.15b yields the stability condition

$$\sqrt[b]{\frac{m}{a(e-mh)}} \geq \frac{b(e-mh)-e}{b(e-mh)-2e}K \tag{C.15c}$$

which cannot be further simplified and therefore is of little practical use.

In summary, cases 1 and 2 combined prove that a feasible system is stable when

$$b > \frac{e}{e-mh}\,, \tag{C.16}$$

which is identical to ineq. C.9. Cases 1 and 2 thus reiterate the derivation of ineq. C.9 and imply that the predator isocline (R^*) is to the left of the minimum in the prey isocline at infinite enrichment (see Fig. 1F). The system can also be stable when ineq. C.16 is reversed (case 3). This includes cases where the prey isocline either does not have a hump or where the predator isocline intersects the prey isocline to the right of the hump. Stability in case 3 must, however, be evaluated numerically.

Literature Cited

Sugie, J., R. Kohno, and R. Miyazaki. 1997. On a predator-prey system of Holling type. Proceedings of the American Mathematical Society 125:2041–2050.