

## GLOBAL STABILITY IN A CLASS OF PREY-PREDATOR MODELS

■ B. S. GOH  
Mathematics Department,  
University of Western Australia,  
Nedlands, W.A. 6009,  
Australia

Global stability is established in a class of prey-predator models. This includes a prey-predator model in which the predator has Type 2 functional response and no intraspecific interactions. Two simple examples demonstrate that Kolmogoroff's theorem does not apply to some members of this class of models.

*1. Introduction.* By global stability in an ecological model we mean stability relative to initial states in which the density of each species is positive. It follows that if a perturbation shifts the state of the system from a feasible equilibrium to a feasible state and the system is thereafter left alone the natural dynamics of the system will drive the state of the system into a neighbourhood of the equilibrium. If a perturbation causes the extinction of a species it is convenient to consider the disturbed system as a new ecosystem of lower dimension. In the absence of immigration the missing species remains extinct. Such catastrophic perturbations of the initial state are excluded in this analysis.

In the literature Kolmogoroff's theorem (1936) has been a very versatile tool for the qualitative analysis of two species interactions. It was used very successfully by Rescigno and Richardson (1973) and May (1974) in their analyses of two species interactions. Recently, Goh (1977) proposed a two-sided energy principle for the construction of Lyapunov functions for population models. This principle states that a viable single species population must on balance absorb energy at low densities and dissipate energy at high densities. In a viable multispecies community there must be a balance in the energy exchanges between the member species and between the species and their environment. The construction of biologically meaningful Lyapunov and

Lyapunov-like functions (Goh, 1978) provides a new tool which is more versatile than Kolmogoroff's theorem. We shall examine examples of two species interactions in which Kolmogoroff's theorem does not apply but in which global stability can be established by means of a Lyapunov function. More importantly the direct method of Lyapunov is applicable to interactions between any number of species but Kolmogoroff's theorem is limited to two species interactions.

2. *Lyapunov Functions for Population Models.* In a model of a viable ecosystem the densities of the interacting species should remain positive as the time variable tends to infinity. But in the standard theory (LaSalle and Lefschetz, 1961) global stability is defined relative to initial states which belong to  $R^n = \{x | (x_1, x_2, \dots, x_n)\}$ . Therefore in order to utilize Lyapunov functions from the standard stability theory we may have to subject them to a preliminary transformation.

Let  $Q$  be a symmetric positive matrix. The quadratic function

$$V(x) = x^T Q x \quad (2.1)$$

is a popular Lyapunov function in the standard stability theory. Let a model of  $m$  interacting species be

$$\dot{N}_i = N_i F_i(N_1, N_2, \dots, N_m) \quad (2.2)$$

where  $N_i$  is the density of the  $i$ th species. Let it have a feasible equilibrium at  $(N_1^*, N_2^*, \dots, N_m^*)$ . To use the function (2.1) as a Lyapunov function of model (2.2) we must first subject it to either one of the transformations,

$$x_i = \ln(N_i/N_i^*), \quad i = 1, 2, \dots, m, \quad (2.3)$$

$$x_i = N_i - (N_i^*)^2/N_i, \quad i = 1, 2, \dots, m, \quad (2.4)$$

or another transformation which maps the positive orthant  $\{N | N_i > 0, i = 1, 2, \dots, m\}$  into the whole of  $R^n$ . From this exercise we note that a Lyapunov function for a population model must tend to infinity as  $N_i \rightarrow 0+$  or  $N_i \rightarrow \infty$  for  $i = 1, 2, \dots, m$ .

*Example 1.* A Lyapunov function for the logistic model  $\dot{N} = (r/K)N(K - N)$  is

$$V(N) = [\ln(N/K)]^2.$$

Along solutions of the model, we have

$$\dot{V}(N) = 2r[\ln(N/K)](K - N).$$

Clearly  $\dot{V}(N) < 0$  for  $K > N > 0$  and  $N > K$ . This implies that the logistic model is globally stable.

Let  $c_1, c_2, \dots, c_m$  be positive constants. A Lyapunov function which is particularly effective for a population model is

$$V(N) = \sum_{i=1}^m c_i [N_i - N_i^* - \ln(N_i/N_i^*)]. \tag{2.5}$$

This function and similar functions (Goh, 1978) are developed specially for population models. Hence by applying the inverse mappings of the transformations, (2.3) and (2.4), we get new Lyapunov functions for problems in which  $x \in R^n$ .

The Lyapunov function  $V(N)$  in (2.5) may be used to establish a region of attraction of an equilibrium of (2.2). It and similar functions may also be used to determine a region of ultimate confinement. If it is used for this purpose it is called a Lyapunov-like function.

*Example 2.* We shall demonstrate the use of Lyapunov-like functions to determine a region of ultimate confinement in a model with three state variables. For models with more than two variables the concept of a region of ultimate confinement is more important than the concept of a limit cycle.

Consider the model,

$$\begin{aligned} \dot{N}_1 &= N_1 [\ln N_2 + (1 - S^2)(S^2 - 2) \ln N_1] \\ \dot{N}_2 &= N_2 [-\ln N_1 + (1 - S^2)(S^2 - 2) \ln N_2] \\ \dot{N}_3 &= N_3 [(1 - S^2)(S^2 - 2) \ln N_3] \end{aligned}$$

where

$$S^2 = (\ln N_1)^2 + (\ln N_2)^2 + (\ln N_3)^2.$$

A Lyapunov-like function for this model is  $V(N) = S^2$ . Along solutions of this model,

$$\dot{V}(N) = 2S^2(1 - S^2)(S^2 - 2). \tag{2.6}$$

This model has a continuum of limit cycles. On the hypersurface  $S^2 = 1$  there is one limit cycle for each value of  $N_3$ .

From (2.6) the region,  $RUC = \{N | V(N) \leq 1\}$ , is a region of ultimate confinement and its region of attraction is  $\{N | V(N) < 2\}$ . This means that every trajectory of the model which initiates in the region RUC will remain indefinitely in it. Moreover every trajectory which initiates in the region  $\{N | 1 < V(N) < 2\}$  will ultimately enter and remain in the RUC region.

For convenience we state the main results in this paper as theorems. Let  $V(N)$  denote the function in (2.5).

*Theorem 1.* Model (2.2) is globally stable in the positive orthant of the state space if (i) it has a feasible equilibrium at  $N^*$ , (ii) there exists positive constants  $c_1, c_2, \dots, c_m$  such that

$$\dot{V}(N) = \sum_{i=1}^m c_i(N_i - N_i^*)F_i(N) \leq 0 \tag{2.7}$$

in the positive orthant and (iii)  $\dot{V}(N)$  does not vanish identically along any solution of the model other than the equilibrium,  $N^*$ .

This theorem follows immediately by using the Lyapunov function  $V(N)$  in (2.5) and LaSalle's extension of the direct method of Lyapunov (see p. 58 of LaSalle and Lefschetz, 1961). It provides a set of sufficient conditions for global stability.

Let  $\beta$  be a positive number. If the conditions of Theorem 1 are only satisfied in the region,  $RAS = \{N | V(N) < \beta\}$ , then RAS is a region of asymptotic stability.

Consider the generalized Lotka–Volterra model,

$$\dot{N}_i = N_i \left[ b_i + \sum_{j=1}^m a_{ij}N_j \right], \quad i = 1, 2, \dots, m. \tag{2.8}$$

The non-trivial equilibrium  $N^*$  satisfies the equation  $AN^* + b = 0$  where  $A = (a_{ij})$  and  $b = (b_i)$ . Substitute this equation into (2.8) we get

$$\dot{N}_i = N_i \sum_{j=1}^m a_{ij}(N_j - N_j^*), \quad i = 1, 2, \dots, m. \tag{2.9}$$

Along solutions of (2.9), inequality (2.7) implies that

$$\dot{V}(N) = (1/2)(N - N^*)(CA + A^TC)(N - N^*) \leq 0 \tag{2.10}$$

where  $C = \text{diag}(c_1, c_2, \dots, c_m)$ . It follows that the Lotka–Volterra model is globally stable if (i) it has a feasible equilibrium, (ii) there exists a positive diagonal matrix  $C$  such that  $CA + A^TC$  is negative semidefinite and (iii)  $\dot{V}(N)$

does not vanish identically along any solution of the model other than the equilibrium.

*Example 3.* Let  $P$  and  $H$  denote predator and prey densities respectively. We shall examine a model of a predator which provides a robust control of a pest (prey). Let  $b, d, e, \alpha_{12}, \alpha_{22}$  be positive constants. Consider the Lotka-Volterra model,

$$\begin{aligned} \dot{H} &= H[b - \alpha_{12}P] \\ \dot{P} &= P[-d + e\alpha_{12}H - \alpha_{22}P]. \end{aligned}$$

The parameter  $e$  is the conversion efficiency of prey into predator;  $b$  is the per capita birth rate of the prey and  $d$  is the per capita death rate of the predator.

In the absence of the predator, the pest (prey) population is unstable. The above model has a unique feasible equilibrium at

$$H^* = (b\alpha_{22} + d\alpha_{12}) / (e\alpha_{12}^2), \quad P^* = b\alpha_{12}.$$

Let  $c_1 = e$  and  $c_2 = 1$ . Condition (2.10) becomes

$$\dot{V} = -\alpha_{22}(P - P^*)^2.$$

Clearly  $\dot{V}$  is negative for all  $(H, P)$  such that  $P > 0, H > 0$  and  $P \neq P^*$ . Hence the model is globally stable.

*3. A Class of Prey-Predator Models.* We shall establish sufficient conditions for global stability in two prey-predator models in which the predator has a Type 2 functional response to changes in the prey density (Holling, 1966; Maynard Smith, 1974). According to Hassell *et al.* (1976), Type 2 functional response is the most common type of functional response among arthropod predators. Another object of this analysis is to provide a warning of the danger which exists in an uncritical application of the statement that Type 2 functional response is destabilizing.

Let  $P$  and  $H$  be predator and prey densities respectively. Let  $a, d, e, w$  be positive constants and  $g(H)$  be the rate of change of the prey density per prey in the absence of the predator. The parameter  $e$  is the conversion efficiency of prey into predator and  $d$  is the mortality rate of the predator. The expression  $aH/(1 + wH)$  is the rate at which the prey is taken by a predator. It is a Type 2 functional response of the predator to prey density. Consider the model,

$$\begin{aligned} \dot{H} &= H[g(H) - aP/(1 + wH)] \\ \dot{P} &= P[-d + eaH/(1 + wH)]. \end{aligned} \tag{3.1}$$

By definition  $(H^*, P^*)$  is a feasible equilibrium of the model if  $H^* > 0, P^* > 0$  and

$$\begin{aligned} g(H^*) - aP^*/(1 + wH^*) &= 0 \\ -d + eaH^*/(1 + wH^*) &= 0. \end{aligned} \quad (3.2)$$

It follows that  $H^* = d/(ea - wd)$  and  $P^* = g(H^*)(1 + wH^*)/a$ . Hence in order that the equilibrium is feasible we must have  $ea > wd$  and  $g(H^*) > 0$ . For convenience, let

$$S = 1/[(1 + wH^*)(1 + wH)]. \quad (3.3)$$

*Theorem 2.* Model (3.1) is globally stable in the feasible region if it has a unique feasible equilibrium at  $(H^*, P^*)$  and

$$(H - H^*)[g(H) - g(H^*) + awSP^*(H - H^*)] < 0 \quad (3.4)$$

for all  $(H, P)$  such that  $H > 0, P > 0$  and  $H \neq H^*$ .

*Proof.* This theorem follows directly from Theorem 1. Substitute (3.2) into (3.1); we get

$$\begin{aligned} \dot{H} &= H[g(H) - g(H^*) - aP/(1 + wH) + aP^*/(1 + wH^*)], \\ \dot{P} &= P[eaH/(1 + wH) - eaH^*/(1 + wH^*)]. \end{aligned} \quad (3.5)$$

Let  $c_1 = (1 + wH^*)/e$  and  $c_2 = 1$ . After some manipulations, condition (2.7) becomes

$$\dot{V}(H, P) = (H - H^*)[g(H) - g(H^*) + awSP^*(H - H^*)]. \quad (3.6)$$

Condition (3.4) implies that  $\dot{V}(H, P)$  is negative for all  $(H, P)$  such that  $H > 0, P > 0$  and  $H \neq H^*$ . By assumption there is only a single equilibrium in the positive quadrant. It follows that the invariant set in the positive quadrant consists of only the equilibrium point. Hence by LaSalle's extension of the direct method of Lyapunov, model (3.1) is globally stable.

*Corollary 2.1.* Let  $\beta$  be a positive number. If condition (3.4) is satisfied only in the region  $V(H, P) < \beta$ , then a region of attraction of  $(H^*, P^*)$  is  $\{(H, P) | V(H, P) < \beta\}$ .

We show by a simple example that it is possible to have global stability when the per capita prey birth rate is not a monotonic decreasing function of prey density. In this case the prey population sustains an Allee effect. It is shown that the same example does not satisfy Kolmogoroff's theorem for global stability.

*Example 4.* Consider the prey-predator model,

$$\begin{aligned} \dot{H} &= H[g(H) - P/(1 + 0.05 H)] \\ \dot{P} &= P[-6/13 + 0.1 H/(1 + 0.05 H)], \end{aligned} \tag{3.7}$$

where  $g(H) = 2 + H(4 - H)/(1 + 2 H)$ . This function has a single hump with the maximum at  $H = 1$ . The model has an equilibrium at  $(6, 1.4)$ .

Condition (3.6) gives

$$\dot{V} = - \frac{(H - 6)^2(0.65 H^2 + 11.7 H + 1.3)}{13(1 + 2H)(1 + 0.05 H)}. \tag{3.8}$$

Hence  $\dot{V}$  is negative for all  $(H, P)$  such that  $H > 0$  and  $P > 0$  and  $H \neq H^* = 6$ . It can be shown that there is only a unique equilibrium in the positive quadrant. It follows that the only invariant point on the line  $H = 6$  and  $P > 0$  is the equilibrium at  $(6, 1.4)$ . Therefore the model is globally stable.

Model (3.7) is of the form  $\dot{H} = HF(H, P)$  and  $\dot{P} = PG(H, P)$ . For this model one of the conditions in Kolmogoroff's theorem is

$$H(\partial F/\partial H) + P(\partial F/\partial P) < 0. \tag{3.9}$$

For (3.7) this inequality requires that

$$H[g'(H) + 0.05 P/(1 + 0.05 H)^2] - P/(1 + 0.05 H) < 0. \tag{3.10}$$

At the point  $(0.5, 0.3)$  the value of the expression on the left hand side of (3.10) is approximately equal to 0.0269. Hence this inequality is violated.

*Example 5.* We shall now demonstrate how Corollary 2.1 may be used to determine a conservative estimate of the region of attraction of a feasible equilibrium in a model.

Let  $d, g_0, g_1, g_2$  be positive constants. Consider the prey-predator model,

$$\begin{aligned} \dot{H} &= H[d + g_0 + g_1 H - g_2 H^2 - P], \\ \dot{P} &= P[-d + H]. \end{aligned} \tag{3.11}$$

This is a special case of model (3.1) with  $w = 0$ . It has a feasible equilibrium at  $(H^*, P^*)$  where  $H^* = d$  and  $P^* = d + g_0 - g_1d - g_2d^2$ .

For this model condition (3.6) becomes

$$\dot{V}(H, P) = (H - d)^2 [g_1 - g_2d - g_2H]. \tag{3.12}$$

If  $d > g_1/g_2$ ,  $\dot{V}(H, P) < 0$  for  $H > 0$  and  $H \neq d$ . In this case model (3.11) is globally stable. If  $g_1/g_2 > d > g_1/(2g_2)$ ,  $\dot{V}(H, P) < 0$  for  $H > (g_1 - g_2d)/g_2$  and  $H \neq d$ . In this case a region of attraction of the equilibrium at  $(H^*, P^*)$  consists of the set of points which satisfy the inequality,

$$V(H, P) < (g_1 - g_2d)/g_2 - d - d \ln [(g_1 - g_2d)/(g_2d)]. \tag{3.13}$$

This follows because in this region  $\dot{V}(H, P)$  is negative if  $H \neq d$ .

We shall establish simple sufficient conditions for global stability in a prey-predator model in which the per capita death rate of the predator is a nonlinear function of its density. In this model the per capita survival rate of the predators, up to a certain density can increase with density because of aggregation which results in enhanced survival from predation by another predator. If this is the case, Kolmogoroff's theorem does not apply because it requires that the per capita rate of increase of the predator decreases monotonically with density.

Consider the prey-predator model,

$$\begin{aligned} \dot{H} &= H[g(H) - aP/(1 + wH)], \\ \dot{P} &= P[f(P) + eaH/(1 + wH)]. \end{aligned} \tag{3.14}$$

Let  $(H^*, P^*)$  be a feasible equilibrium of this model and let  $S$  denote the function in (3.3).

*Theorem 3.* Model (3.14) is globally stable in the feasible region if it has a feasible equilibrium at  $(H^*, P^*)$  and if

$$\begin{aligned} (H - H^*)[g(H) - g(H^*) + awSP^*(H - H^*)] \\ + (P - P^*)[(1 + wH^*)/e][f(P) - f(P^*)] < 0 \end{aligned} \tag{3.15}$$

for all  $(H, P)$  such that  $H > 0, P > 0$  and  $(H, P) \neq (H^*, P^*)$ .

This theorem follows directly from Theorem 1 with  $c_1 = (1 + wH^*)/e$  and  $c_2 = 1$ . The expression in (3.15) is none other than  $\dot{V}(H, P)$  computed along solutions of (3.14). Hence when it is negative for  $H > 0, P > 0$  and  $(H, P) \neq (H^*, P^*)$ , model (3.14) is globally stable.



*Example 6.* Consider the prey-predator model

$$\begin{aligned}\dot{H} &= H[g(H) - P/(1 + 0.05 H)] \\ \dot{P} &= P[f(P) + 0.1 H/(1 + 0.05 H)]\end{aligned}\quad (3.16)$$

where  $f(P) = -0.4156 + P(1 - P)/(1 + 8P)$  and  $g(H) = 2 + H(4 - H)/(1 + 2H)$ . The function  $f(P)$  has a maximum at  $P = 0.25$ . For  $0.25 > P > 0$ , the function  $f(P)$  is monotonic increasing and hence the second expression in (3.16) violates one of the conditions in Kolmogoroff's theorem.

Model (3.16) has a feasible equilibrium at (6, 1.4). We have

$$\dot{V} = -\frac{(H-6)^2(0.65H^2 + 11.7H + 1.3)}{13(1+2H)(1+0.05H)} - \frac{(P-1.4)^2(0.4+12.2P)}{(1+8P)}. \quad (3.17)$$

Clearly  $\dot{V}$  is negative in the positive quadrant other than at the equilibrium (6, 1.4). Hence model (3.16) is globally stable in the feasible region.

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