Canad. Math. Bull. Vol. 18 (3), 1975

STABILITY OF CERTAIN DYNAMICAL SYSTEMS

BY
CLARK JEFFRIES

Introduction. For n real variables $\{x_i\}$ of time t we consider the following equations:

$$dx_i/dt = \sum_{j=1}^{n} a_{ij}(x, t) f_j(x_j) \tag{1}$$

Throughout $\{a_{ij}\}$ and $\{f_i\}$ are assumed to be continuous. For any given initial conditions there is assumed to be at least one trajectory solution. We assume $f_j(0)=0$ (so $\mathbb{O}=(0, 0, \ldots, 0)$ is a critical state), $f_j(u)$ has the same sign as u otherwise, and $\lim_{v\to\pm\infty} \int_0^v f_j(u)\,du=+\infty$. Two cases which will be mentioned below are $f_j(u)=u$ and $f_j(u)=\exp(u)-1$. The purpose of this note is to develop criteria for the (neutral or asymptotic) stability of (1) at $\mathbb{O}$.

Result. We will prove the following

THEOREM. *Suppose*

(i) *for each* x, t, i *that* $a_{ii}(x, t)\le 0$,

(ii) *for each* x, t, $i\ne j$ *that either* $a_{ij}(x, t)=a_{ji}(x, t)=0$, *or* $a_{ij}(x, t)\ne 0$, $a_{ji}(x, t)\ne 0$, *and* $a_{ij}(x, t)/a_{ji}(x, t)$ *is a negative constant independent of* x, t, *and*

(iii) *for each* x, t *and each set of three or more distinct indices* $i, j, k, \ldots, p$ *that* $|a_{ij}, a_{jk}, \ldots, a_{pi}|=|a_{ip}, \ldots, a_{kj}, a_{ji}|$.

Then $\mathbb{O}$ *is a stable critical point for* (1), *and all trajectories for* (1) *may be bounded in terms of initial conditions for* x.

Proof. Define n positive real numbers $\{\lambda_i\}$ as follows. Let $\{i, j, \ldots\}$ be the set of indices of variables which interact with x_1. (A variable x_i interacts with x_1 if there is some x, t such that $a_{i1}(x, t)\ne 0$, or alternatively, $a_{1i}(x, t)\ne 0$.) If the set of such indices is empty, let $\lambda_1=1$ and start over with x_2. Otherwise, for each such index i let $\lambda_1=1$, $\lambda_i=-\lambda_1 a_{ji}/a_{i1}$, where for each i we choose x, t so that $a_{i1}(x, t)\ne 0$. Using condition (ii) each such λ_i is constant and we abbreviate by $\lambda_i=-\lambda_1 a_{1i}/a_{i1}$. Next consider the (possibly empty) set of all indices $\{k, l, \ldots\}$ of variables which interact with at least one of $\{x_i, x_j, \ldots\}$. Define for new indices $\{\lambda_k, \lambda_l, \ldots\}$ by $\lambda_k=-\lambda_i a_{ik}/a_{ki}$. Condition (iii) implies that this scheme is consistent. For suppose x_2 and x_3 interact with x_1 and with each other. Then we must have $\lambda_2=-\lambda_1 a_{12}/a_{21}$

Received by the editors June 25, 1974 and, in revised form, September 18, 1974.

and $\lambda_3 = -\lambda_1 a_{13}/a_{31}$. Also we have $\lambda_3 = -\lambda_2 a_{23}/a_{32}$, precisely because of condition (iii). So it goes for all loops of three or more interacting variables. That is, this scheme may be extended to those variables which interact with $\{x_k, x_l, \ldots\}$, and so on. When a maximal set of variables containing x_1 is so obtained, start over with some other variable, if any, and so on. The final result is a set of positive numbers $\{\lambda_i\}$ such that if $i \neq j$ and x_i and x_j interact, then $\lambda_i a_{ij} = -\lambda_j a_{ji}$ for x, t such that $a_{ij} \neq 0$, $a_{ji} \neq 0$, and so for all x, t. If $i \neq j$ and x_i and x_j do not interact, then $\lambda_i a_{ij} = -\lambda_j a_{ji}$ nonetheless. So for all $i \neq j$, x, t we have $\lambda_i a_{ij} = -\lambda_j a_{ji}$, that is, $\lambda_i^{1/2} a_{ij} \lambda_j^{-1/2} = -\lambda_j^{1/2} a_{ji} \lambda_i^{-1/2}$. To summarize this paragraph we may say that the conditions are sufficient to guarantee the existence of n positive constants $\{\lambda_i\}$ such that the similarity transformation on $\{a_{ij}\}$ by the diagonal matrix with $\lambda_i^{1/2}$ in the i,i-entry renders $\{a_{ij}\}$ into skew form plus non-positive diagonal entries for each x, t.

Next define a Liapunov function $\varphi(x)$ as

$$\varphi(x) = \sum_{i=1} \lambda_i \int_0^{x_i} f_i(u)\, du$$

Clearly $\varphi(x) > 0$ unless $x = \mathbb{O}$. Clearly $\varphi(x)$ strictly increases without bound on all radial lines in n-space away from $\mathbb{O}$. Finally,

$$\begin{aligned} d\varphi/dt &= \sum_{i=1}^{n} \lambda_i f_i(x_i)\, dx_i/dt \\ &= \sum_{i=1}^{n} \sum_{j=1}^{n} [\lambda_i^{1/2} f_i(x_i)] \lambda_i^{1/2} a_{ij}(x, t) \lambda_j^{-1/2} [\lambda_j^{1/2} f_j(x_j)] \\ &= \sum_{i=1}^{n} a_{ii}(x, t) \lambda_i f_i(x_i)^2 \leq 0 \end{aligned}$$

so $\varphi(x)$ is non-increasing along all trajectories. The level sets of $\varphi(x)$ are homeomorphic to $(n-1)$-spheres centered about $\mathbb{O}$. Hence any trajectory for (1) may be bounded by the initial state x in n-space. Q.E.D.

Discussion. The case $f_j(u) = u$ is particularly simple and of mathematical interest. However, if $f_j(u) = N_j(e^u - 1)$, $N_j > 0$, then the theorem is relevant to theoretical ecology. Making the change of variables $y_i = N_i \exp x_i$ we have

$$dy_i/dt = \sum_{j=1}^{n} y_i \tilde{a}_{ij}(y, t)(y_j - N_j) \tag{2}$$

where $\tilde{a}_{ij}(y, t) = a_{ij}(x, t)$. This is a direct generalization of the Lotka-Volterra equations with critical state $(N_1, N_2, \ldots, N_n)$ [1]. Notice that $\{\tilde{a}_{ij}\}$ satisfies conditions (i), (ii), (iii) if and only if $\{a_{ij}\}$ satisfies the same conditions. Thus if $\{\tilde{a}_{ij}\}$ satisfies the conditions, $(N_1, N_2, \ldots, N_n)$ must be a stable critical state for (2). We state the above as a

Corollary. *If* $\tilde{a}_{ij}$ *satisfies conditions* (i), (ii), (iii), *then* $(N_1, N_2, \ldots, N_n)$ *is a stable critical state for* (2).

The corollary may be interpreted as follows in mathematical ecology. Suppose the dynamics of an ecosystem may be expressed in the form (2), fulfilling the conditions. Condition (i) means that intraspecific interactions are of the self-regulating type. Condition (ii) means that for each pair of species and each x, t there is either no interaction or an interaction of the predator-prey or parasite-host type. It is possible with condition (ii) that two species might interact only at certain x, t, say, only in the absence of a preferred prey or only at certain times of the year. Condition (ii) would not allow, however, one species to affect a second species without the second species affecting the first. For example, condition (ii) would not allow a predator to kill its prey without benefiting from the kill. Should, say, a preferred prey become abundant, the effects of a given predator and given prey per animal on each other would both be reduced. Condition (ii) requires that such reductions be proportional.

Condition (iii) means that if for some x, t loops exist in the food web of the ecosystem, then the loops must be in a sense balanced. For example, suppose zooplankton are preyed upon by both cod and capelin and that cod prey upon capelin. This constitutes a loop in the Arctic Ocean food web. If the system may be modeled as (2), then for stability we might expect the absolute value of the products of the interaction coefficients of the two cycles to be equal.

It is important to note that such equality is invariant of rescaling. Given (2) suppose we define new variables $z_i=\gamma_i y_i$, $\gamma_i>0$. Then we have

$$dz_i/dt=\sum_{j=1}^{n} z_i\hat{a}_{ij}(z,t)(z_j-\hat{N}_j) \tag{3}$$

where the new coordinates of the critical state are $\hat{N}_j=\gamma_j N_j$ and the new interaction matix is $\hat{a}_{ij}(z,t)=\tilde{a}_{ij}(y, t)\gamma_j^{-1}$. Note that $\{\hat{a}_{ij}\}$ fulfills the conditions if and only if $\{\tilde{a}_{ij}\}$ fulfills the conditions.

ACKNOWLEDGEMENT. I am grateful to the referee for her or his helpful suggestions.

REFERENCE

1. Curtis Strobeck, *N Species Competition.* Ecology **54** (1973), 650–654.

DEPARTMENT OF MATHEMATICS
UNIVERSITY OF SASKATCHEWAN
SASKATOON, SASKATCHEWAN
S7N 0W0

PRESENT ADDRESS:
GENERAL DELIVERY
MESSINIPE, SASKATCHEWAN

https://doi.org/10.4153/CMB-1975-067-8 Published online by Cambridge University Press