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- <sup>1</sup> Chen, S. H., and Giblett, E. R., *Science*, **173**, 148 (1971).  
<sup>2</sup> Someren, H. van., Meera Khan, P., Westerveld, A., and Bootsma, D., *Nature new Biol.*, **240**, 221 (1972).

## Connective stability of complex ecosystems

IN 1970, Garner and Ashby<sup>1</sup> asked an important question: "If a large system is assembled (connected) at random, or has grown haphazardly, should we expect it to be stable or unstable?" They showed on a linear model that probability of stability generally decreases with the increase of the degree of connectedness among the parts of the system. This fact was confirmed by May<sup>2</sup> in a study of large systems in the ecological context.

Here I now report that a wide class of linear and non-linear time-varying large systems have been identified<sup>3,4</sup>, which are stable in spite of changes in the degree of connectedness among the parts (subsystems) of the system. A large system is considered connectively stable if it is stable (in the sense of Liapunov) for any degree of connectedness among the subsystems. The connective property of stability can be established in the systems with competitive equilibrium<sup>5</sup>, which appear as useful models in such diverse fields as biology<sup>6</sup> and the arms race<sup>7</sup>, economics<sup>5,8</sup> and transistor circuits<sup>9</sup>.

The development of the connective stability concept can be best illustrated on the linear model used in (refs 1 and 2):

$$\frac{dx}{dt} = Ax$$

where  $x = \langle x_1 \ x_2 \ \dots \ x_n \rangle$  is an  $n$  vector and  $A = (a_{ij})$  is an  $n \times n$  constant matrix. I assume that  $A$  has negative diagonal elements<sup>1</sup>, and non-negative off-diagonal elements, that is

$$a_{ij} \begin{cases} < 0, & i=j \\ \geq 0, & i \neq j \end{cases}$$

The above system is stable if (and only if) the matrix  $A$  satisfies the Hicks conditions:

$$a_{11} < 0, \begin{vmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{vmatrix} > 0, \dots, (-1)^n \begin{vmatrix} a_{11} & a_{12} & \dots & a_{1n} \\ a_{21} & a_{22} & \dots & a_{2n} \\ \dots & \dots & \dots & \dots \\ a_{n1} & a_{n2} & \dots & a_{nn} \end{vmatrix} > 0$$

I allow off-diagonal elements  $a_{ij}$  to be time-varying, and replace them with  $e_{ij}a_{ij}$ , where  $e_{ij} = e_{ij}(t)$  are arbitrary functions such that

$$0 \leq e_{ij}(t) \leq 1$$

Therefore, the elements  $e_{ij}(t)$  of the  $n \times n$  interconnection matrix  $E = (e_{ij})$  measure the coupling from  $x_i$  to  $x_j$  and represent disconnection when  $e_{ij}(t) = 0$  at any time  $t$ . It has been shown<sup>4,8</sup> that, under Hicks conditions, stability of the system is invariant to changes in any (and all)  $e_{ij}(t)$  and that the system is connectively stable.

In an ecological system,  $x$  is the vector of the populations  $x_i$  and the elements  $a_{ij}$  of the matrix  $A$  represent the effect of the  $j$ th species on the  $i$ th species in the neighbourhood of the equilibrium. Non-negativity of the off-diagonal elements  $a_{ij}$  ( $i \neq j$ ) implies (gross) symbiotic interactions among species. Negativity of the diagonal  $a_{ii}$ s means that each species is density dependent or 'stabilized'<sup>2</sup>. Both restrictions on the sign of  $a_{ij}$ s can be removed at the expense of more refined analysis. By applying the Hicks conditions to the McKenzie's diagonal form of  $A$ , the off-diagonal  $a_{ij}$ s can have arbitrary signs and connective stability of the ecosystem with mixed (competitive - predator - symbiotic - saprophytic) interactions among species can still be established. The restriction  $a_{ii} < 0$  can be removed by considering species in the stable 'blocks' (subsystems) and using the decomposition-aggregation methods<sup>3,4,8</sup> to conclude stability of the overall system by Hicks conditions. The decomposition-aggregation analysis can take advantage of special structural 'block' properties of ecosystems<sup>2</sup>. Furthermore, it is possible to demonstrate<sup>4</sup> wide tolerances to nonlinearities in the interactions of stable

ecosystems reflected by non-linear elements  $a_{ij} = a_{ij}(t, x)$  of the system matrix  $A = A(t, x)$ .

By increasing the magnitude of the off-diagonal elements  $a_{ij}$  and thus the interaction complexity of the ecosystem, the Hicks conditions are eventually violated. Since the conditions are both necessary and sufficient for stability, by reaching the critical values of  $a_{ij}$ s as determined by the Hicks inequalities, a sharp transition from stability to instability takes place. Therefore, there is an analytical basis<sup>3,4,8</sup> for verification of the important Garner-Ashby conjecture<sup>1</sup> and the equally significant May's experiment<sup>2</sup>.

The recursive nature of the Hicks conditions suggests that individual parts of the system can be decomposed from each other and again composed together randomly in various ways without affecting stability. It should be noted, however, that Hicks conditions are valid only for the constant matrix  $A$ . Kamke's comparison principle and vector Liapunov functions from the theory of differential inequalities<sup>10</sup> are needed to extend the validity of Hicks conditions to matrices with time varying elements and to give a rigorous proof<sup>4,8</sup> of this intuitive result.

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<sup>1</sup> Garner, M. R., and Ashby, W. R., *Nature*, **228**, 784 (1970).

<sup>2</sup> May, R. M., *Nature*, **238**, 413-414 (1972).

<sup>3</sup> Šiljak, D. D., *IEEE Trans.*, SMC-2, 657-663 (1972).

<sup>4</sup> Šiljak, D. D., *IEEE Trans.*, SMC-3, 415-417 (1973).

<sup>5</sup> Arrow, K. J., and Hahn, F. H., *General Competitive Analysis* (Holden-Day, San Francisco, 1971).

<sup>6</sup> Keyfitz, N., *Introduction to Mathematics of Population*, (Addison-Wesley, Reading, Massachusetts, 1968).

<sup>7</sup> Richardson, L. F., *Arms and Insecurity*, (Boxwood Press, Pittsburgh, 1960).

<sup>8</sup> Šiljak, D. D., *Proc. 1973 IEEE Conf. Decision and Control, San Diego*, 265-275 (New York, 1973).

<sup>9</sup> Sandberg, I. W., *Bell Syst. Tech. J.*, **48**, 35-54 (1969).

<sup>10</sup> Lakshmikantham, V., and Leela, S., *Differential and Integral Inequalities, I*, (Academic Press, New York, 1969).

## Palatability dynamics of cardenolides in the monarch butterfly

THE adaptive strategy of sequestering cardiac glycosides from milkweed plants (Asclepiadaceae and Apocynaceae) has evolved in several taxa of insects<sup>1</sup>. Since these cardenolides elicit vomiting following ingestion, birds learn to avoid the insects on sight after one or more emetic experiences<sup>2</sup>. By a specific assay, we found a spectrum of cardenolide concentrations in adult monarch butterflies (*Danaus plexippus* L., Danainae) collected during the autumnal migration from four areas in eastern North America<sup>3</sup>. In this communication we compare Atlantic with Pacific Coast monarch populations and explore quantitative relationships between cardenolide concentrations and palatability spectra. The latter were measured by our blue jay (*Cyanocitta cristata bromia* Oberholser, Corvidae) emetic dose fifty (ED<sub>50</sub>) test<sup>4</sup>.

Migrating East Coast butterflies were netted in September 1971 in the floodplain of the Connecticut River in Northampton and Hockanum, Massachusetts. Those from the West Coast came from three overwintering colonies in California during November 1971 at Muir Beach, Natural Bridges State Park at Santa Cruz, and at the Academy of Music at Santa Barbara. All butterflies were frozen until oven dried and individually ground for analysis as before<sup>3</sup>. Cardenolide concentrations were measured from February to June 1972. Because there were no significant concentration differences between the California populations, they were combined for statistical analyses.