

matters arising

Stability of Lotka–Volterra systems

IN our recent paper in this journal, we claimed that global stability was a consequence of the negative-definiteness of a matrix $B = (A + A')/2$. The subsequent argument was accurate to the extent that if B is found to be negative-definite, then the system must be locally and globally stable. Since A is taken to be an arbitrary matrix, however, it is possible that A can be stable while B is not negative-definite. This means that there may be some locally stable systems that are not globally stable.

The arguments and conclusions are therefore modified as follows. Let d_i be a set of n strictly positive numbers. Introduce the Liapunov function

$$V(x) = \sum_i 2d_i[\exp(x_i) - x_i - 1]$$

which has time derivative $dV/dt = u'(DA + A'D)u$ where u is the vector with elements $[\exp(x_i) - 1]$, and D is a matrix with diagonal elements d_i and zeros elsewhere. This allows us to state the following theorem: if there exists a strictly positive diagonal matrix D such that $(DA + A'D)$ is negative-definite, the Lotka–Volterra system is simultaneously locally and globally stable.

It is not possible to say that all locally stable states are globally stable. The criterion of the previous paragraph is in general a sufficiency condition, not a necessity condition. The criterion does identify the largest known subset of locally stable states that are also globally stable. This is the strongest result available on global stability so far.

Some interesting, if enigmatic, features are worth noting. First, setting $D = I$, the unit matrix, our theorem shows that negative-definiteness of the symmetric part of the community matrix A is sufficient to ensure local and global stability. Second, if $D = N^*$, negative-definiteness of the symmetric part of the interaction matrix α which has elements a_{ij} is also sufficient to ensure local and global stability. Third, the theorem stated above identifies a subset of the possible matrices A which is also D -stable². This means that for this subset stability depends only on the interaction matrix α and is independent of the precise value of N^* , so long as all N_i^* are strictly positive. Such an identification

is in accord with intuitive feelings about the relationship between the geometry of the isoclines of the Lotka–Volterra systems and the flow in phase space.

Finally, there is a strong connection with qualitative (or sign) stability³, which involves the analysis of interaction matrices α where only the signs of the interaction elements are known. Our theorem above shows directly that Lotka–Volterra models which have sign stable interaction matrices α with strictly negative diagonal elements have globally stable dynamics.

Since submitting this manuscript the error in our original paper has independently been pointed out to us by Dr. H. I. Freedman, Department of Mathematics, University of Alberta. In addition Drs. Granero-Porati and Zanua, Institute of Physics, Parma questioned our use of a community matrix with elements $(a_{ij}N_i^*)$; however we pointed out that such matrix has the same eigen values as a matrix with elements $(N_i^*a_{ij})$.

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¹ Tuljapurkar, S. D., and Semura, J. S., *Nature*, 257, 388–389 (1975).

² Barnett, S., and Storey, C., *Matrix Methods in Stability Theory* (Barnes and Noble, New York, 1970).

³ Quirk, J., and Ruppert, R., *Rev. Econ. Studies*, 32, 311–326 (1965).

Relatedness

ALTHOUGH the article by Dawkins and Carlisle¹ points out relevant questions regarding desertion, it also perpetuates a misconception concerning relatedness. In their example, a female with enough food to support only one infant must choose between two infants the same age, an orphaned baby brother and her own son. They conclude “Intuition points to the son but this is not necessarily correct. There are no genetic grounds for preferring either infant: the mother’s relatedness to both is the same, 0.5.” There is, however, a genetic difference! The degree of relatedness between two siblings is only on the average 0.5, in any particular instance it may be much less or much greater than that. Additional assumptions are required to state that behaviour is based on average relatedness. Although it could hardly be considered to prove anything, the intuitive

response to save the offspring might, in fact, indicate that nature prefers a sure thing (relatedness=0.5 as in the case of the son) to gambling (average relatedness=0.5 as in the case of the siblings). In addition, in the example they used, even the average relatedness was \neq 0.5. Assuming a dioecious diploid organism whose parents are not related, opposite sexed siblings are actually somewhat <50% related on average since they must necessarily have one sex determining chromosome which is not in common. Similarly, siblings of the same sex are on average somewhat >50% related.

It should be noted that the validity of their conclusions is not affected by this correction.

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¹ Dawkins, R., and Carlisle, T. R., *Nature*, 262, 131–133 (1976).

DAWKINS REPLIES—Gibson¹ is right, both in the main point she makes and in her observation that it doesn’t matter anyway. But her gambling analogy is misleading.

She thinks of the offspring as a safe bet while the sibling is a risky gamble. Yes, setting aside Gibson’s trivial point about sex chromosomes, it is true that exactly 50% of the genome of a parent is inherited by a given child, while siblings share 50% of their genomes only on average. But who cares about genomes? Certainly not natural selection, at least in sexual populations². From the point of view of a single altruistic gene sitting in the body of an individual, a particular child of that individual is just as risky a prospect as a particular sibling. The gene may or may not be present in the body of the offspring, and it may or may not be present in the body of the sibling. It is a 50% gamble in both cases.

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¹ Gibson, P. A. K., *Nature*, 264, 381 (1976).

² Dawkins, R., *The Selfish Gene* (Oxford University Press, 1976).