

Table 2 Acute Toxicity of Di-*n*-butyl Phthalate to Four Species of Fish

Species	Temperature (°C)	TL ₅₀ * (µg/l.)		
		24 h	48 h	96 h
Fathead minnow (<i>Pimephales promelas</i>)	17	—	1,490	1,300
Bluegill (<i>Lepomis macrochirus</i>)	17	1,230	731	731
Channel catfish (<i>Ictalurus punctatus</i>)	17	3,720	2,910	2,910
Rainbow trout (<i>Salmo gairdneri</i>)	12	—	—	6,470

Toxicity was measured by standard static bioassay.

*The tolerance limit is the concentration in which 50% of fish survive for a specified time.

centration (0.1 µg/l.), respectively, within 14 days. Only 6% of residual di-2-ethylhexyl phthalate remained in the scud after 10 days in fresh water.

Di-2-ethylhexyl phthalate was examined for reproductive effects in zebra fish (*Brachydanio rerio*) and guppies (*Poecilia reticulata*) by dietary exposure. Zebra fish were fed diets containing 50 and 100 µg/g of food and guppies were fed 100 µg/g. Up to 88.5% of the zebra fish fry died before foraging began as compared with a 50% mortality in control fish. All the dying fry exposed to di-2-ethylhexyl phthalate died in tetany, which suggests that this compound may alter normal calcium metabolism. However, tetany did not occur in the dying controls. Intraperitoneal injections of di-2-ethylhexyl phthalate (3 µg/kg) increased serum calcium, decreased serum potassium, but did not affect serum sodium and chloride in coho salmon (*Oncorhynchus kisutch*). All of the adult guppies fed di-2-ethylhexyl phthalate became lethargic after 2 months of exposure and an 8% incidence of abortions was noted in this group. Continuous exposure of waterfleas (*Daphnia magna*) to 3 µg/l. of di-2-ethylhexyl phthalate significantly ($P < 0.05$) reduced reproduction by 60%. Details of these studies will be published separately.

The incidence of phthalate esters in fish seemed to be greater in aquatic areas associated with industrial and heavily populated regions, although hatchery and farmed fish fed diets contaminated with the esters also contained residues. Dietary contamination was probably a consequence of the use of contaminated fish products in feeds. Residues of phthalate esters previously reported in milk⁸ and bovine tissues^{9,10} may have resulted from dietary intake of phthalate esters. Phthalate esters have also been found in deep sea jellyfish¹¹ and soil¹². The actual amounts and distribution of these pollutants in the environment have not been fully investigated, but a recent report of 100 mg/l. phthalate esters in a water sample from the Ohio River, West Virginia, was not anticipated (R. Sandridge, personal communication).

The acute toxicity of phthalate esters seems relatively insignificant, but there are indications that these compounds can be detrimental to aquatic organisms at low chronic concentrations. They are produced in large amounts, they are in wide use as plasticizers, and, by some means, they are entering aquatic ecosystems. Thus, these compounds should be considered as environmental pollutants and a more detailed evaluation of toxicological effects of phthalate esters is essential to elucidate their impact on these systems.

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GENERAL

Will a Large Complex System be Stable?

Gardner and Ashby¹ have suggested that large complex systems which are assembled (connected) at random may be expected to be stable up to a certain critical level of connectance, and then, as this increases, to suddenly become unstable. Their conclusions were based on the trend of computer studies of systems with 4, 7 and 10 variables.

Here I complement Gardner and Ashby's work with an analytical investigation of such systems in the limit when the number of variables is large. The sharp transition from stability to instability which was the essential feature of their paper is confirmed, and I go further to see how this critical transition point scales with the number of variables n in the system, and with the average connectance C and interaction magnitude α between the various variables. The object is to clarify the relation between stability and complexity in ecological systems with many interacting species, and some conclusions bearing on this question are drawn from the model. But, just as in Gardner and Ashby's work, the formal development of the problem is a general one, and thus applies to the wide range of contexts spelled out by these authors.

Specifically, consider a system with n variables (in an ecological application these are the populations of the n interacting species) which in general may obey some quite nonlinear set of first-order differential equations. The stability of the possible equilibrium or time-independent configurations of such a system may be studied by Taylor-expanding in the neighbourhood of the equilibrium point, so that the stability of the possible equilibrium is characterized by the equation

$$dx/dt = Ax \quad (1)$$

Here in an ecological context x is the $n \times 1$ column vector of the disturbed populations x_j , and the $n \times n$ interaction matrix A has elements a_{jk} which characterize the effect of species k on species j near equilibrium^{2,3}. A diagram of the trophic web immediately determines which a_{jk} are zero (no web link), and the type of interaction determines the sign and magnitude of a_{jk} .

Following Gardner and Ashby, suppose that each of the n species would by itself have a density dependent or otherwise stabilized form, so that if disturbed from equilibrium it would return with some characteristic damping time. To set a time-scale, these damping times are all chosen to be unity: $a_{jj} = -1$. Next the interactions are "switched on", and it is assumed that each such interaction element is equally likely to be positive or negative, having an absolute magnitude chosen

from some statistical distribution. That is, each of these matrix elements is assigned from a distribution of random numbers, and this distribution has mean value zero and mean square value α . (For a fuller account of such a formulation, see refs. 2 and 3.) α may be thought of as expressing the average interaction "strength", which average is for simplicity common to all interactions. In short,

$$\mathbf{A} = \mathbf{B} - \mathbf{I} \quad (2)$$

where \mathbf{B} is a random matrix, and \mathbf{I} the unit matrix. Thus we have an unbounded ensemble of models, one for each specific choice of the interaction matrix elements drawn individually from the random number distribution.

It is important to note that randomness only enters in the initial choice of the coefficients a_{jk} , which then define a particular model. Once the dice have been rolled to get a specific system, the subsequent analysis is purely deterministic.

The system (1) is stable if, and only if, all the eigenvalues of \mathbf{A} have negative real parts. For a specified system size n and average interaction strength α , it may be asked what is the probability $P(n, \alpha)$ that a particular matrix drawn from the ensemble will correspond to a stable system. For large n , analytic techniques developed for treating large random matrices may be used to show* that such a matrix will be almost certainly stable ($P \rightarrow 1$) if

$$\alpha < (n)^{-1/2} \quad (3)$$

and almost certainly unstable ($P \rightarrow 0$) if

$$\alpha > (n)^{-1/2} \quad (4)$$

The transition from stability to instability as α increases from the regime (3) into the regime (4) is very sharp for $n \gg 1$; indeed the relative width of the transition region scales as $n^{-2/3}$.

Such a precise answer for any model in the ensemble in the limit $n \gg 1$ is a consequence of the familiar statistical fact that, although individual matrix elements are liable to have any value, by the time one has an $n \times n$ matrix with n^2 such statistical elements, the total system has relatively well defined properties.

Next we introduce Gardner and Ashby's connectance, C , which expresses the probability that any pair of species will interact. It is measured as the percentage of non-zero elements in the matrix, or as the ratio of actual links to topologically possible links in the trophic web. The matrix elements in \mathbf{B} now either, with probability C , are drawn from the previous random number distribution, or, with probability $1 - C$, are zero. Thus each member of the ensemble of matrices \mathbf{A} corresponds to a system of individually stable parts, connected so that each part is affected directly by a fraction C of the other parts. For large n , $\alpha^2 C$ plays the role previously played by α^2 , and we find the system (1) is almost certainly stable ($P(n, \alpha, C) \rightarrow 1$) if

$$\alpha < (nC)^{-1/2} \quad (5)$$

and almost certainly unstable ($P \rightarrow 0$) if

$$\alpha > (nC)^{-1/2} \quad (6)$$

* From equation (2) it is obvious that the eigenvalues of \mathbf{A} are $\lambda - 1$, where λ are those of \mathbf{B} . The "semi-circle law" distribution for the eigenvalues of a particular random matrix ensemble was first obtained by Wigner⁴, and subsequently generalized by him to a very wide class of random matrices whose elements all have the same mean square value⁵. Although the matrix \mathbf{B} does not in general possess the hermiticity property required for most of these results to be directly applicable, the present results for the largest eigenvalue and its neighbourhood can be obtained by using Wigner's⁴ original style of argument on $(\mathbf{B}^N)(\mathbf{B}^N)^*$ where N is very large. Indirectly relevant is Mehta⁵ and Ginibre⁶.

It is interesting to compare the analytical results with Gardner and Ashby's computer results for smallish n . (Their choice of \mathbf{A} differs slightly from ours, but in essence they have the fixed value $\alpha^2 = 1/3$, and diagonal elements intrinsically -0.55 rather than -1 .) Although our methods are based on the assumption that n is large, and are therefore only approximations when applied to $n=4, 7, 10$, the two approaches in fact agree well when compared, being not more than 30% discrepant even for $n=4$.

The central feature of the above results for large systems is the very sharp transition from stable to unstable behaviour as the complexity (as measured by the connectance and the average interaction strength) exceeds a critical value. This accords with Gardner and Ashby's conjecture.

Applied in an ecological context, this ensemble of very general mathematical models of multi-species communities, in which the population of each species would by itself be stable, displays the property that too rich a web connectance (too large a C) or too large an average interaction strength (too large an α) leads to instability. The larger the number of species, the more pronounced the effect.

Two corollaries are worth noting, although they should not be taken to have more than qualitative significance.

First, notice that two different systems of this kind, with average interaction strengths and connectances α_1, C_1 and α_2, C_2 respectively, have similar stability character if

$$\alpha_1^2 C_1 \approx \alpha_2^2 C_2 \quad (7)$$

Roughly speaking, this suggests that within a web species which interact with many others (large C) should do so weakly (small α), and conversely those which interact strongly should do so with but a few species. This is indeed a tendency in many natural ecosystems, as noted, for example, by Margalef⁷: "From empirical evidence it seems that species that interact feebly with others do so with a great number of other species. Conversely, species with strong interactions are often part of a system with a small number of species. . . ."

A second feature of the models may be illustrated by using Gardner and Ashby's computations (which are for a particular α) to see, for example, that 12-species communities with 15% connectance have probability essentially zero of being stable, whereas if the interactions be organized into three separate 4×4 blocks of 4-species communities, each with a consequent 45% connectance, the "organized" 12-species models will be stable with probability 35%. That is, of the infinite ensemble of these particular 12-species models, essentially none of the general ones are stable, whereas 35% of those arranged into three "blocks" are stable. Such examples suggest that our model multi-species communities, for given average interaction strength and web connectance, will do better if the interactions tend to be arranged in "blocks"—again a feature observed in many natural ecosystems.

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