physiological reaction[2] suggest a less trivial explanation. As experiments with *Lytechinus* were performed in the absence of added ATP, the decrease in calcium affinity which results from removal of ATP in *Echinus* may well be the factor responsible for the apparent differences in calcium affinity in the two species.

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Fusion or lysis of vesicles by Ca^{2+}?

GINSBERG showed[1] that sonicated phosphatidylserine (PS) vesicles in the presence of large concentrations of Ca^{2+} or Mg^{2+} did not retain sucrose and he concluded that the final structures had lost the form of closed vesicles. As such, he proposes the cation effect to be one of lysis and the Ca^{2+}–PS system to be an inappropriate one for the study of membrane fusion. It is not surprising that the final product of the PS–metal interaction cannot retain solutes such as sucrose, as the vesicles collapse and internal volume is lost[2]. The PS membrane repeat determined by X-ray diffraction is 53 Å in 2 mM Ca^{2+}; 67 Å in 10 mM Mg^{2+} (ref. 2) and 71 Å in 1 M Na^{+} (ref. 3). The term 'membrane fusion' refers to the formation of larger membranous structures by contact and mixing of the parent membranes. This is in contrast to the mixing of membrane lipids by diffusion of the components, as proposed for the dimyristoyl lecithin–dipalmitoyl lecithin system[4]. Recent experiments[3] have shown that release of contents is nearly second order in vesicle concentration and is concomitant to aggregation, demonstrating vesicle contact in leakage experiments. That Ca^{2+} induces fusion, that is, mixing of membrane components, is indicated by the formation of large cochleate structures, which on addition of EDTA, become huge vesicles capable of entrapping large molecules[5]. Mg^{2+} alone is less effective[6] but in its presence, only small concentrations of Ca^{2+} are required for obtaining larger structures[2,3]. Similarly, in the dimyristoyl phosphatidylglycerol–dipalmitoyl phosphatidylglycerol vesicles[7] and in phosphatidic acid–phosphatidylcholine vesicles[8], Ca^{2+} induces mixing of the lipids, that is, fusion. Our view is that fusion requires a destabilisation of the membranes in contact until the joint membrane is arranged. Model systems are intended to be approximations to the *in vivo* systems. A definition of membrane fusion as a process without leakage is too restrictive and so far no experiment has ruled out leakage in fusion events. In model systems better approximating the *in vivo* system, such as mixed PA/PC vesicles[8], mixing and retention of contents has been demonstrated. The interactions postulated to occur between the Ca^{2+} and PS in the pure system are still relevant to the mixed systems.

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GINSBERG AND GINGELL REPLY—The comments of Nir and Pangborn stem from an inadequate definition of membrane fusion. They claim that fusion is equivalent to the mixing of components from two contacting parent membranes. However, physiological membrane fusion apparently involves the transfer of aqueous contents from one membrane-bounded compartment to another without spillage into inappropriate spaces, as seen in phagosome–lysosome interaction and secretion. Any artificial system should fulfil this additional criterion to be biologically relevant[1,2]. Thus, the X-ray data cited by these authors[3] seem to invalidate their PS system as a paradigm for membrane fusion: Ca^{2+} converts PS into a multilayer containing no removable water. Such collapsed multilayers could result from the lysis of closed membranous forms by the mechanism we suggest[1]. The experiments described by Nir and Pangborn where loss of contents is reported to accompany vesicle aggregation may also be explained in terms of lysis: Ca^{2+}-induced vesicle rupture with loss of contents may provide the antecedent for immediate aggregation of the resultant membrane fragments.

Although Ca^{2+} is strongly implicated in biological membrane fusion[4], there is no compelling reason to suppose that its action on dispersions of single acidic phospholipids resembles its interaction with mixed lipid membranes nor with the biomembrane systems in which fusion was first studied[5]. This point is underlined by the far greater Ca^{2+} sensitivity of natural vesicle fusion[6]. Gershfeld has recently shown[7] that sonicated vesicles are in a metastable state at temperatures exceeding the lipid phase transition temperature. Thus, addition of divalent cations to PS vesicle suspensions may merely trigger a return to equilibrium by a variety of unknown pathways.

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Some real communities are unstable

THE mathematical stability analyses of randomly constructed food webs of Pimm and Lawton[1,2] have emphasised the destabilising influence of omnivory. Their examination of a number of real food webs[3] seems to support their hypothesis that webs with many omnivores should be rare except in insect host–parasitoid systems. However, I analysed the real food webs cited as corroborative by Pimm and Lawton, that is, those of Askew[4], Force[5] and Richards[6], and found that none meet the criterion for Lyapunov stability. The validity of the models and their inherent assumptions appears questionable.

All webs were analysed using the observed signs of interaction and Pimm and Lawton's constraints on the selection of random magnitudes for parasitoid–host and herbivore–plant interactions. Signs for variable interaction, species A and B each serving as prey or predator for the other, were arbitrarily assigned. To investigate whether the occurrence of self-limited species influenced stability, runs were repeated with self-regulation terms removed (all principal diagonal elements equal to zero). Finally, self-limitation was introduced at the lowest trophic level (plant), a criterion used by Pimm and Lawton in constructing their random webs. Analysis of Richard's web was performed twice, once with the parasitoid–host and again with vertebrate predator–prey constraints used for the predatory arthropods. In no case were any of 50 runs for either the original or adjusted webs stable.

I included only primary interactions in abstracting a matrix from Force's web. The excluded terms (dashed lines in Force's paper[5]) represent secondary interactions, such as the rejection of a potential host which has been previously

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