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Characterization of Virulent Bacteriophage Infections of Escherichia coli in Continuous Culture

There are several points in the article by Horne (*1*) on bacteriophage infections in continuous culture which deserve comment. He reported only measurements of plaque titers and of viable bacteria but was able to note changes in both the bacteria and phage with time. We have studied a very similar system of *Escherichia coli* B with T2 phage in which a more detailed population analysis was performed (*2, 3*). It was shown that resistant strains increased dramatically, but sensitive organisms persisted as a significant proportion of the total cells. Although Horne states that no regular pattern could be discerned in the first 20 to 40 hours, we observed a definite relationship in which bacterial peaks and declines were followed by corresponding fluctuations in phage titer.

Although there are probably differences in the behavior between T2 phage and the T3 and T4 phages studied by Horne, he described only one new type of phage appearing, whereas we noted several distinct phage mutants based on plaque morphology (*3*). In contrast to the parent organism, our T2 resistant bacterial cells formed mucoid colonies on nutrient agar and could not be infected by high concentrations of stock T2 phage. Resistant cells had the common property of having thick capsules, but the sensitive cells showed none. However, capsulation of a culture prior to infection was found to offer only partial protection against phage attack (*4*).

Although Horne successfully maintained his systems for very long periods of time, we think that his dilution rate (0.04 hr^{-1}) was relatively low so that his observations were complicated by the presence of too many cells not in the active growth phase, a condition necessary for phage production. Furthermore, many significant details of population behavior were missed by not distinguishing between the various types of cells present. Viable cells, total cells, infected cells, sensitive uninfected cells, and resistant cells can all be measured, and such data do elucidate the evolution of cell types. The systems are much more complex than Horne's limited data would suggest.

Many investigators use chemostat to refer to a continuous culture system, but to avoid confusion, we are of the opinion that this bacterium-phage culture was not in chemostasis as implied by the title of the article.

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My report (*1*) gave some preliminary findings of a study which investigated the usefulness of this system as a model of host-parasite, prey-predator situations, to which it has many analogies and where mathematical formulation is simplified by the absence of a search component. Emphasis was placed on the effects on the components of the population of selection over very extended periods of time (*2*). The published data were of populations growing at a low rate chosen as typical of some natural and seminatural habitats of these organisms where many bacterial cells may be growing extremely slowly (*3*), a condition which does not preclude phage growth. However, populations of *Escherichia coli* B and phages T3 and T4r have been grown at higher dilution rates (0.16 hr^{-1}). These similarly come to an equilibrium, the stability of which increases with time; they differ from slower growing populations by maintaining relatively higher titers of the phage component during each stage of the interaction. Inverse correlations of phage and bacterial numbers are common in the early stages of such interactions [figure 1 in (*1*)], but *regularity* of the amplitude and frequency of the cycles, even after an extended period of coevolution, is not found and is probably not to be expected where the potential rates of increase of the two components are so very different.

That coevolution of the components of these populations involves several successive changes in the relationship of bacterial resistance and phage host-range is generally accepted (*4*). Many hundreds of phage-resistant mutants (*5*) and of phage host-range mutants (*6*) have been isolated. A frequent characteristic of the former is a "watery" or "mucoid" appearance of the colony (*5*).

Evidence of the heterogeneity of the phage component in continuous culture populations is reflected in the diverse plaque morphology which is a normal feature of the early stages of the interaction. However, here the usefulness of such mutants is limited since mutations expressed as differences in plaque morphology do not necessarily correspond to differing abilities of the phage to reproduce in the selected populations. Also the extreme minuteness of plaques isolated from later stages of the interaction—reported not as a new mutant of the phage T3 but as a characteristic of all T-series phages grown in such populations and probably resulting from an accumulation of many mutations affecting the reproductive capacity of the phage—makes categorization of the phage mutants by plaque morphology unsatisfactory.

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