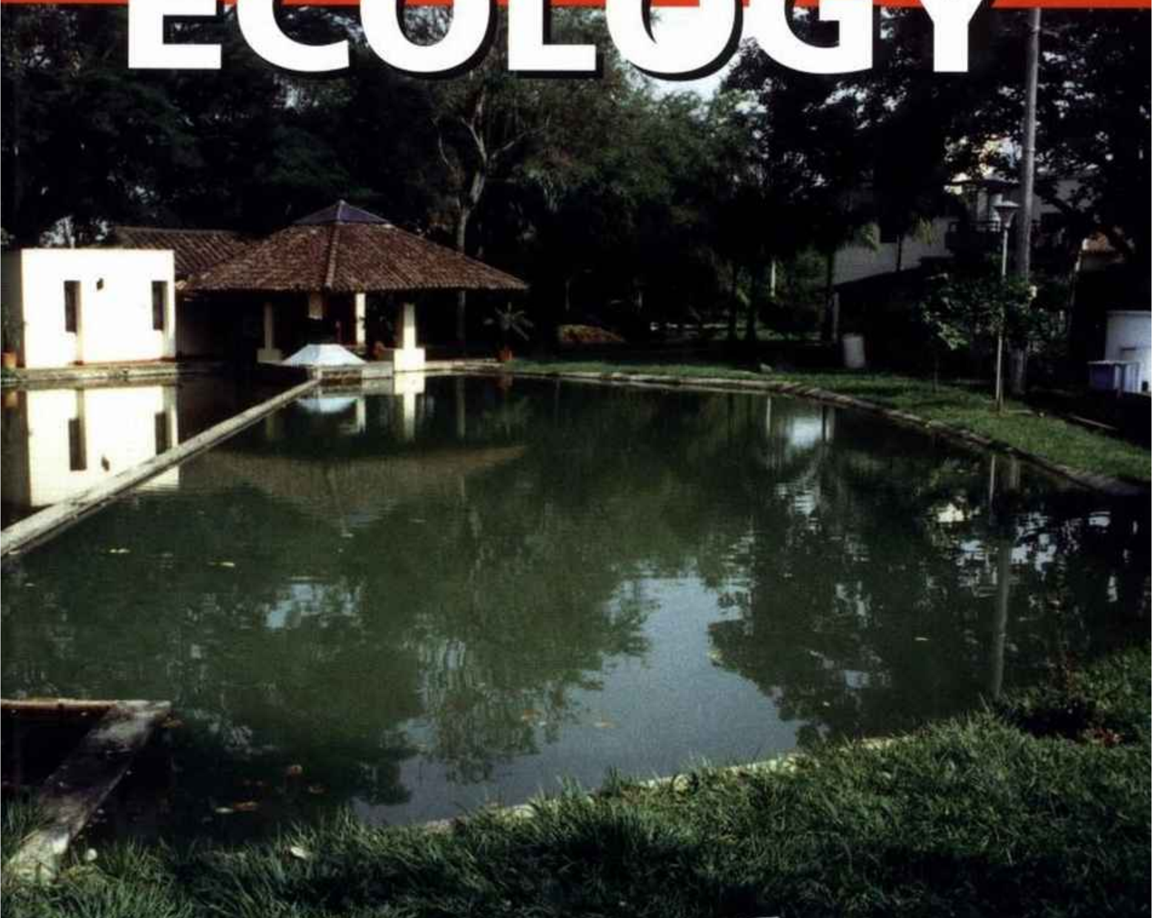
VIRAL ECOLOGY



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To my children Allen and Rachel

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Preface

Virology is a field of study that has grown and expanded greatly since the viruses as a group first received their name in 1898. Many of the people presently learning virology have come to perceive these acellular biological entities as trinkets of nucleic acid to be cloned, probed, and spliced. However, viruses are much more than trinkets to be played with in molecular biology laboratories. Indeed, they are highly evolved biological entities with an organismal biology that is complex and interwoven with the biology of their hosting species.

The purpose of this book is to define and explain the ecology of viruses, that is, to examine what life might seem like from a "virocentric" point of view as opposed to our normal "anthropocentric" perspective. As we begin our examination of virocentric life, it is important to realize that in nature both the viruses of macroorganisms and the viruses of microorganisms exist in cycles with their respective hosts. Under normal conditions, the impact of viruses on their natural host populations may be barely apparent due to such factors as evolutionary coadaptation between the virus and those natural hosts. However, when viruses find access to new types of hosts and alternate transmission cycles, or when they encounter a concentrated population of susceptible genetically similar hosts such as occurs in densely populated human communities, communities of cultivated plants or animals, or algal blooms, then the impact of the virus on its host population can appear catastrophic. The key to understanding these types of cycles lies in understanding the viruses and how their ecology relates to the ecology of their hosts, their alternate hosts, and any vectors they utilize, as well as their relationship to the availability of suitable vehicles that can transport the different viral groups.

This book would have reached its audience a year earlier if one of the echoviruses had not invited itself into my brain to cause encephalitis. But, since these members of the genus *Enterovirus* usually just maim their hosts, rather than killing them outright, the book finally has seen completion. I wish to thank the many authors who contributed to this book, and I offer special appreciation to Noreen J. Adcock, who kindly assisted me by editing Chapters 1 and 2.

As required, I must hereby state that the United States of America's Environmental Protection Agency was not involved with the preparation of this book.

Christon J. Hurst

I

Structure and Behavior of Viruses: An Introduction

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1

Defining the Ecology of Viruses

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I. INTRODUCTION

The purpose of this book is to define the ecology of viruses and, in so doing, try to approach the question of what life is like from a "virocentric" (as opposed to our normal anthropocentric) point of view. Ecology is defined as the branch of

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science that addresses the relationships between an organism of interest and the other organisms with which it interacts, the interactions between the organism of interest and its environment, and the geographic distribution of the organism of interest. The objective of this chapter is to introduce the main concepts of viral ecology. The remaining chapters of this book will then address those concepts in greater detail and illustrate the way in which those concepts apply to various host systems.

A. What Is a Virus?

Viruses are biological entities that possess a genome composed of either ribonucleic acid (RNA) or deoxyribonucleic acid (DNA) (Campbell *et al.*, 1997; Eigen, 1993; Strauss and Strauss, 1999). Viruses are infectious agents that do not possess a cellular structure of their own, and hence are "acellular infectious agents." Furthermore, the viruses are obligate intracellular parasites, meaning that they live (if we can say that about viruses) and replicate within living host cells at the expense of those host cells. Viruses accomplish their replication by usurping control of the host cell's biomolecular machinery. Those that are termed "classical viruses" will form a physical structure termed a "virion," which consists of their RNA or DNA genome surrounded by a layer of proteins (termed "capsid proteins"), which form a shell or "capsid" that protects the genomic material. Together, this capsid structure and its enclosed genomic material are often referred to as being a "nucleocapsid." The genetic coding for the capsid proteins generally is carried by the viral genome. Most of the presently known virus types code for their own capsid proteins. However, there are some viruses that are termed as being "satellite viruses." The satellite viruses encapsidate with proteins that are coded for by the genome of another virus that coinfects (simultaneously infects) that same host cell. The virus that loans its help by giving its capsid proteins to the satellite virus is termed as being a "helper virus." The capsid or nucleocapsid is, in the case of some virus groups, surrounded in turn by one or more concentric lipid bilayer membranes obtained from the host cell. There exist many other types of acellular infectious agents that have commonalities with the classical viruses in terms of their ecology. Two of these other types of acellular infectious agents — the viroids and prions — are included in this book and are addressed within their own respective chapters (9 and 16). Viroids are biological entities akin to the classical viruses and likewise can replicate only within host cells. The viroids possess RNA genomes but lack capsid proteins. The agents that we refer to as prions were once considered to be nonclassical viruses. However, we now know that the prions appear to be aberrant cellular protein products that, at least in the case of those afflicting mammals, have acquired the potential to be environmentally transmitted. The natural environmental acquisition of a prion infection occurs when a susceptible host mammal ingests the bodily material of an infected host mammal. The reproduction of prions is not a replication, but rather seems to result from a conversion of a normal host protein into an abnormal form (Prusiner, 1997; Vogel, 1997).

B. What Is Viral Ecology?

Ecology is the study of the relationships between organisms and their surroundings. Therefore, Viral ecology is the relationship between viruses, other organisms, and the environments that a virus must face as it attempts to comply with the basic biological imperatives of genetic survival and replication. As shown in Figure 1,

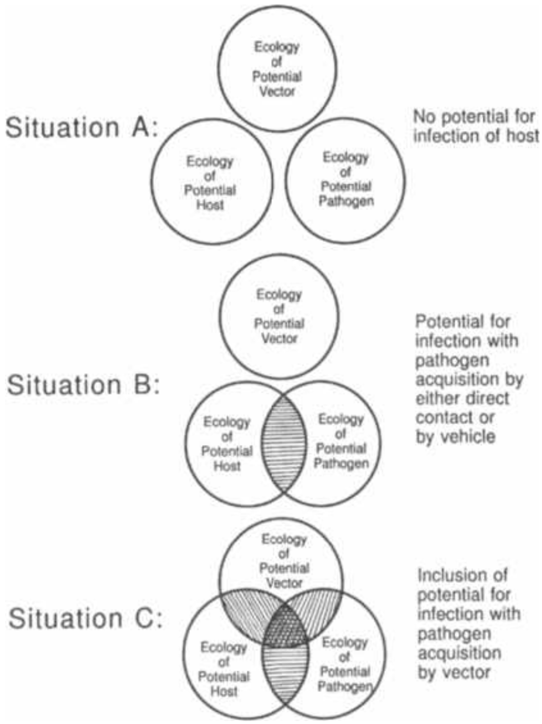

Fig. 1. Interactions between organisms (biological entities) occur in areas where the physical and chemical ecologies of the involved organisms overlap. Infectious disease is a type of interaction in which a microorganism acts as a parasitic predator. The microorganism is referred to as a pathogen in these instances.

interactions between species and their constituent individual organisms (biological entities) occur in the areas where there exist overlaps in the temporal, physical, and biomolecular (or biochemical) aspects of the ecological zones of those different species. Many types of interactions can develop between species as they share an environment. One of the possible types of interactions is predation. When a microorganism is the predator, it is referred to as being a pathogen and the prey is referred to as being a host.

When we study viral ecology, we can view the two genetic imperatives that every biological entity must face — namely, that it survive and that it reproduce — in the perspective of a biological life cycle. A generalized biological life cycle is depicted in Figure 2. In its most basic form, this type of cycle exists at the level of the individual virus or individual cellular being. However, it must be understood that, in the case of a multicellular being, this biological life cycle exists not only at the level of each individual cell, but also at the tissue or tissue system level, as well as at the organ level. This biological life cycle likewise exists on even larger scales, where it operates at levels that describe the existence of each species as a whole, at the biological genus level, and also seems to operate further upward to at least the biological family level. Ecologically, the life cycles of those different individuals and respective species that affect one another will become interconnected temporally, geographically, and biologically. Thus, there will occur an evolution of the entire biological assemblage, and this process of biotic evolution will in turn be obliged to adapt to any abiotic changes that occur in the environment that those organisms share. While the physiologic capacities of a species establish the potential limits of the niche that it could occupy within this shared environment, the actual operational boundaries of its niche are more restricted and defined by its interspecies connections and biological competitions.

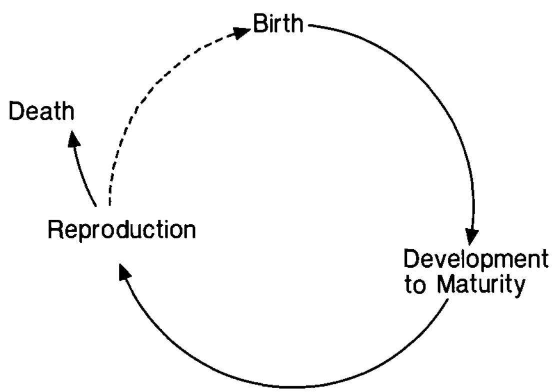

Fig. 2. Generalized biological life cycle. Ecologically, the life cycles of different organisms that affect one another are temporally interconnected.

C. Why Study Viral Ecology?

The interplay that occurs between a virus and the living organisms that surround it, while all simultaneously pursue their own biological drive to achieve genetic survival and replication, creates an interest for studying the ecology of viruses (Doyle, 1985; Fuller, 1974; Larson, 1998; Morell, 1997; Packer, 1997; Preston, 1994; Zinkernagel, 1996). While examining this topic, we improve our understanding of the behavioral nature of viruses as predatory biological entities. It is important to realize that in nature the viruses of both macroorganisms and microorganisms normally exist in a cycle with their respective hosts. Under normal conditions, the impact of viruses on their natural hosts may be barely apparent due to factors such as evolutionary coadaptation between the virus and its host (evolutionary coadaptation is the process by which species try to achieve a mutually acceptable coexistence by evolving in ways that enable them to adapt to one another). However, when viruses find access to new types of hosts and alternate transmission cycles, or when they encounter a concentrated population of susceptible genetically similar hosts such as occurs in densely populated human communities, communities of cultivated plants or animals, or algal blooms, then the impact of the virus on its host population can appear catastrophic (Nathanson, 1997; Subbarao *et al.*, 1998).

As we study viral ecology, we come to understand not only those interconnections that exist between the entities of virus and host, but also the interconnections between these two entities and any vectors or vehicles that the virus may utilize (Cooper, 1995; Nathanson, 1996). As shown in Figure 3, this interplay can be represented by the four vertices of a tetrahedron. The possible routes by which a virus may move from one host organism to another can be illustrated as the

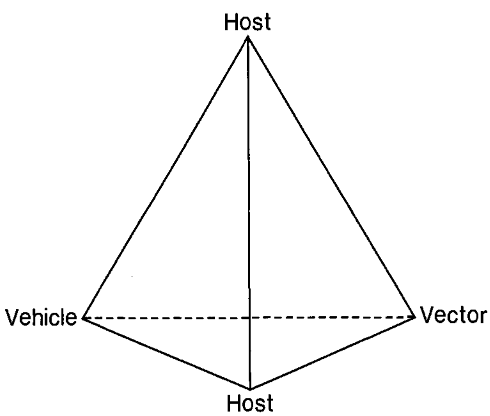

Fig. 3. The lines connecting the four vertices of this tetrahedron represent the possible routes by which a virus can move from one host organism to another.

interconnecting lines between those vertices, which represent two hosts (present and proximate) plus one vertex apiece representing the concepts of vector and vehicle. Figure 4, which represents a flattened form of the tetrahedron shown in the Figure 3, can be considered our point of reference as we move forward in examining viral ecology. The virus must survive when in association with the present host and then successfully move from that (infected) host organism (center of Fig. 4) to another host organism (Cooper, 1995). This movement, or transmission, may occur via direct contact between the two host organisms or via routes that involve vectors and vehicles (Cooper, 1995; Hurst and Murphy, 1996). By

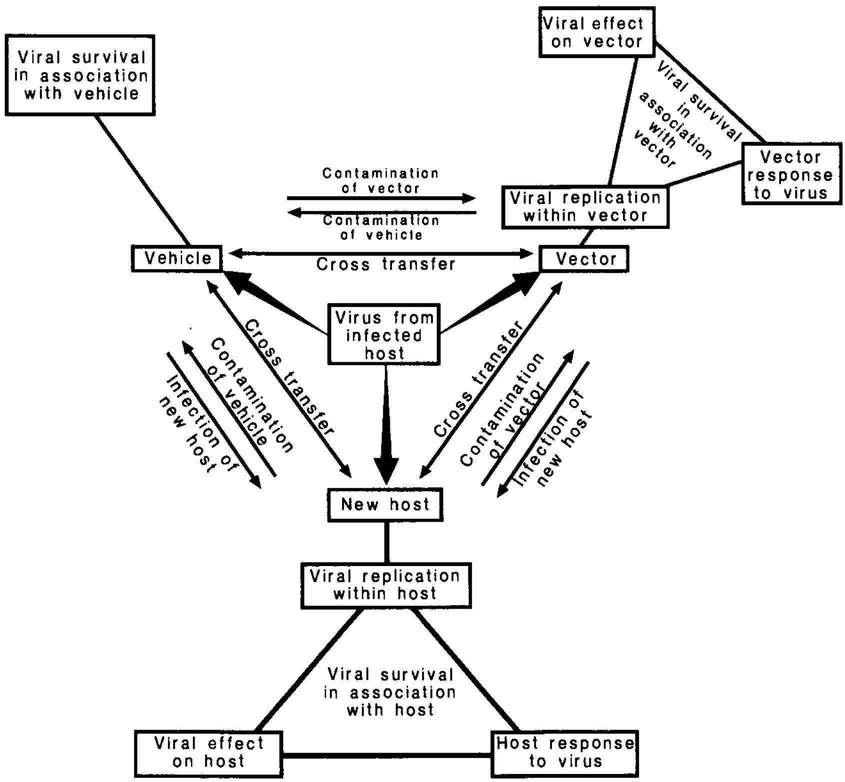

Fig. 4. Viral ecology can be represented by this diagram, which depicts a flattened form of the tetrahedron shown in Figure 3. The virus must successfully move from an infected host organism to another host organism. This movement, or transmission, may occur via direct transfer or via routes that involve vehicles and vectors. To sustain this cycle of transmission within a population of host organisms, the virus must survive when in association with the subsequently encountered hosts, vehicles, and vectors.