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Source: Journal of Wildlife Diseases, 6(4) : 236-238

Published By: Wildlife Disease Association

URL: <https://doi.org/10.7589/0090-3558-6.4.236>

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Some Vertebrate Host Aspects of Arbovirus Ecology

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With arbovirus organisms, as with other forms of life, preservation of the "species" has a high priority. A host specificity which is too narrow, a mechanism of overwintering in temperate areas which is too uncertain, or a means of dispersal which is too restricted all would make survival of an arbovirus tenuous, particularly since viremia in the vertebrate host lasts only a few days. Arbovirus epizootics are dependent for support upon the availability of a considerable number of susceptible vertebrate hosts, some with rapid replacement rates, since once infected, the animal dies or becomes immune and participates no more in virus propagation. The hosts must also be in a favorable association with the essential arthropod vectors.

Arboviruses seem to have evolved a dual system of propagation: the first, an enzootic or consuetudinal system defined as a gradually evolved, well-balanced habitual relationship of the parasite with its regular hosts, possibly but not necessarily including a vector; the second, an epizootic or amplifier host system favoring spectacular vector-borne spread, either in a long-lived alternate host population which has become non-immune or in a short-lived alternate host population during its annual peak.

An epidemic or epizootic is not necessarily a favorable event for the viral parasite. Epidemics and epizootics usually run their course quickly and result in the removal by death or immunity of large numbers of susceptible hosts from the infection system. In a relatively short time transmission to additional hosts becomes difficult, the epizootic comes to a halt and the virus essentially disappears from the affected area. The apparent favorable survival feature is an extension of range beyond that available to the arbovirus at the onset of the epizootic. A situation appearing more suitable for the parasite is an endemic or enzootic one with the virus passing more slowly from host to host, keeping pace with, but not surpassing, the reproductive rate of the host.

The amplifier system presents such a spectacular pattern of epizootic virus spread that it has been the most studied aspect of arbovirus ecology, frequently to the exclusion of investigations on the more basic consuetudinal system. The high vector and host infection rates common to epizootics are probably not necessary in enzootic situations to assure virus maintenance. Quite likely a vector species appearing less "efficient" in terms of susceptibility and transmitting capability might be the most suitable as an enzootic vector. Likewise, a less "efficient" vertebrate host, in terms of viremia levels attained and infectivity for vectors, may be the best partner in the consuetudinal state.

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Some recent ecological observations of Venezuelan equine encephalitis (VEE) virus affirm consuetudinal maintenance involving mammals in primary roles. South Florida exemplifies an area where VEE is silently maintained. VEE has never been recorded in epidemic form in south Florida, and the disease in horses is unknown there. In fact, activity of the virus was totally unsuspected until 1960¹ when antibody was detected in a high proportion of the adult Seminole Indians of the Big Cypress Reservation about 40 miles south of Lake Okechobee. Later, virus isolations were obtained from everglades mosquitoes.² The first human clinical case was not detected until two years ago,³ and this was in the southeast corner of Florida rather than at the Reservation. Field studies showed that the virus is maintained consuetudinarily on some of the hammocks or "islands" of the south Florida everglades, about 75 miles south of Big Cypress. Endemicity on the hammocks is indicated by antibody rates in the rodents averaging about 50% and by presence of virus in the *Melanoconion* mosquitoes throughout the year. Birds were essentially antibody negative.⁴ A low rate of antibody in long-lived animals, such as deer, bobcats and raccoons, to the north of the endemic zone indicates that the virus may occasionally extend beyond the everglades.

A similar ecology of VEE is apparent on the Guajira peninsula of Venezuela where the virus was first recognized,⁵ but there, equines were involved in the amplifier-epidemic phase. The area is semi-desert, and burros are disproportionately abundant. Rains are infrequent, but when they do come, large broods of *Aedes* mosquitoes are produced. Inland from the dry coastal area are two large swamps, one near Sinamaica and the other near Paraguaipoa. These swamps harbor cotton rats, raccoons and opossums, and could likely be the sites of consuetudinal maintenance of the virus year after year. Apparently the virus escapes occasionally from the contained swamp cycle and spreads among the burros throughout the entire arid zone. This epizootic spread occurs about every 4-5 years,⁶ just about as often as the immune burros from a past epidemic are replaced by the young non-immunes. After the epizootic has depleted the stock of susceptibles, the virus again subsides to its permanent foci and continues its silent existence.

Similar situations are envisioned in other geographic areas where occasional outbreaks of VEE have occurred, for example, in Guatemala in 1969. In July an equine epizootic began on the tropical Pacific coastal plain, presumably stemming from fresh water swamps, and extended through the temperate mountain valleys. There is little doubt that in this epizootic spread, the equines themselves served as virus amplifiers since wild mammals were scarce throughout this highly populated, over-grazed region, and only equines and a calf yielded virus isolations in laboratory tests. The virus has now subsided, undoubtedly to its consuetudinal swamp-inhabiting hosts and vectors, probably not to spread again over the same territory for several years.

Eastern, western or St. Louis encephalitis (EE, WE, SLE) viruses are believed by modern investigators to have consuetudinal systems to maintain themselves throughout the year and between epizootic years. Since these are largely avian viruses, it appears logical to assume that the enzootic hosts are birds. However, it is possible that other vertebrates may instead serve in this capacity. For example, it has been shown experimentally that reptiles may have long-lasting viremias following inoculation of WE virus,^{7,8} and the virus has also been reported from wild-caught snakes⁹ and amphibians.⁹ Low isolation rates do not necessarily minimize the importance of these animals as reservoirs, since even infrequent infections may in nature be adequate to spark seasonal virus buildup in amplifier hosts. Certainly the role of cold-blooded animals as consuetudinal hosts is worthy of further investigation. The possibility of vectors other than mosquitoes maintaining year-around virus should also be taken into consideration.

The viruses of EE and WE in birds illustrate well how effective an amplifier system can be in dispersal of arboviruses. Migratory birds can carry virus southward in autumn¹⁰ and northward in the spring.¹¹ There is little doubt that this free movement assures thorough seeding of these viruses within receptive areas of the flight range. Although Casals' discovery of differences between tropical and North American strains of EE¹² is evidence against seasonal transport being mandatory for maintenance of these viruses in nature, one cannot but feel that such free movement year after year assures wide distribution and virus perpetuation. Also, much may remain to be learned about the stability or plasticity of virus strains upon passage through various vertebrate hosts and vectors which may influence interpretation of Casals' data.

Productive studies on consuetudinal systems of arbovirus maintenance should include both laboratory and field investigations. The findings of each will indicate the direction for further research: field association of viruses with particular vertebrates and arthropods in interepidemic periods will suggest reservoir systems; experimental infection and virus maintenance studies in the laboratory will confirm their feasibility.

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