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THE EPIDEMIOLOGY OF FOX RABIES IN EUROPE

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Rabies virus is a very old parasite of animals and humans. Records dating back to 2300 years BC document that rabies was prevalent and recognized as a disease transmitted from dogs to humans in ancient Babylon, with the same epidemiologic features as today. Rabies virus strains from such divergent hosts as bats or foxes show very strong cross-reaction in serum neutralization in all parts of the world. This would suggest that rabies virus has not substantially changed in 4000 years of observation. Recently, Wiktor and Koprowski (1) demonstrated strain differences by the use of monoclonal antibodies. However, this method has not yet been applied to epidemiologic studies.

How can such a disease agent, which usually kills its host, survive? Two basic features of rabies appear to play a key role in the perpetuation of the virus: one is the peculiar pathway of infection which in most infected animals avoids the stimulation of an immune response until late in the fatal course of the disease (2), thus preventing the creation of an immune population (3, 4), and the other is the high dependence on the population density of the main vector species, where the chain of infection is interrupted long before the host species becomes extinct (5–8).

In this review we give an account of the epidemiology of fox rabies in Europe and try to explain the intimate links between the dynamics of the disease and the biology and ecology of foxes. The typical pattern of the rabies epizootic has stimulated the development of computer simulations. Some of these approaches have been discussed by Toma and Andral (9) and will not be included in this review.

THE SPREAD OF RABIES

Starting from endemic foci in northwestern Poland (10, 11), a rabies epizootic whose main vector is the fox (12) has spread east, south and west. It has invaded large parts of central, eastern and western Europe in the last 40 years (figure 1) (13, 14). Figure 2 shows the geographic distribution of rabies outbreaks occurring during the last quarter of 1979 (20) in central and western Europe. Only limited information is available on the eastward spread into the Union of Soviet Socialist Republics (USSR). Moving from Poland and the Kalinin district into Lithuania and Latvia, the epizootic reached Estonia in 1968. Byelorussia and the Ukraine were invaded after 1963.

According to Selimov et al. (72), a second focus of infection was observed simultaneously in the Astrakhan region of the Volga delta, from which rabies spread in eastern, northern and western directions. Natural foci of fox rabies are found today in the Baltic republics, Byelorussia, Russian Socialist Republic south 56° latitude from Kaliningrad to the Khabarovsk region, in the Ukraine and Kasachstan.

Fox rabies thus far has reached Poland, the USSR, the German Democratic Re-

Abbreviations: IC, intracerebral; IM, intramuscular; $MICLD_{50}$, mouse intracerebral 50 per cent lethal dose.

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