THE ECOLOGY OF SYLVATIC RABIES IN THE SOUTHEASTERN UNITED STATES: A REVIEW

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ABSTRACT

This report summarizes existing information on the ecology of rabies in wildlife in the southeastern United States. Patterns of involvement of various wildlife species and their significance in the ecology of rabies are discussed. Other subjects that are discussed include factors involved in epizootics, barriers to interspecific spread, and various mechanisms which may maintain the rabies virus in populations during periods between epizootics.

INTRODUCTION

Wildlife biologists are well aware of the importance of disease in the ecology, economics and management of wildlife species. The recent increase in interest among public health workers concerning wild animals as reservoirs of diseases infective to man and domestic animals has added significance to wildlife diseases as a consideration in management. (See, for example: Abdussalam, 1959; Thompson, 1961; Shield, 1966; and Saulmon, 1966.) Wildlife biologists should be well informed so they can be in a position to advise public health workers on wildlife ecology and combat misguided demands for extreme and unnecessary control or eradication of wildlife.

During studies of the biology of the raccoon, I became interested in the potential significance of diseases of this species, and conducted an extensive study of the literature relating to certain diseases of wild carnivores. This report summarizes for the general wildlife biologist results of recent research on the ecology and epizootiology of rabies in wildlife.

Rabies, or hydrophobia, is a disease that is almost cosmopolitan in distribution, and it affects nearly all warm-blooded animals. It is caused by a filterable virus that is found in the saliva of infected animals.

PROCEDURE

Published reports were located by searching all volumes of the following indexes and journals:

American Journal of Veterinary Research
Bulletin of the Wildlife Disease Association
Index Veterinarius
Journal of the American Veterinary Medical Association
Journal of Infectious Diseases
Journal of Mammalogy
Journal of Wildlife Management
Proceedings of Annual Meetings of the U. S. Livestock Sanitation Association
Public Health Reports
Wildlife Abstracts
Wildlife Review

Literature Cited sections of all publications reviewed were examined for additional references. Papers dealing exclusively with clinical aspects, control measures, and rabies in domestic animals were generally excluded, as were many popular articles. Information was also obtained from surveillance reports of the National Communicable Disease Center and from correspondence and discussions with personnel of the National Rabies Laboratory, the University of Georgia School of Veterinary

Medicine, the Auburn University School of Veterinary Medicine, the Alabama Department of Public Health, and the Florida Board of Health.

CHARACTERISTICS OF REPORTED INCIDENCE

Host Involvement

Two types of rabies are recognized: sylvatic (wild animal) and dog rabies. These are distinguished solely on the basis of epizootiology. Different immunological strains of rabies virus probably exist, but they have not been identified (Tierkel, 1959).

Sylvatic rabies may manifest itself as a raging epizootic, as a long-term enzootic or as isolated, sporadic cases. Epizootics in the United States have characteristically involved foxes and striped skunks with incidental occurrence in other species.

Johnson (1965) cites historical evidence from the Old World indicating that rabies is primarily a disease of wild animals and that domestic animals are aberrant hosts. However, rabies was not reported in wild animals in most of the southeastern United States until about 30 years ago when a major epizootic occurred (Johnson, 1945; Moore, 1950; Wood, 1954; and Frederickson and Thomas, 1965). Since that time, there has been a steady increase in reported cases of sylvatic rabies while cases in domestic animals have declined rather sharply as a result of control programs. During 1968, 75 per cent of the recorded cases of rabies in the United States were in wild animals. (1968 figures on incidence of rabies are from the National Communicable Disease Center Rabies Summary, 1968.)

It is not known whether the recent increase in reported cases of sylvatic rabies in the United States reflects a real increase in incidence or if it is due to improved surveillance techniques and greater awareness of wildlife hosts. It should be emphasized that surveillance data are in most cases inadequate indexes to the prevalence of rabies. The number of reported cases is not so much related to the incidence of rabies as to the number of people in the area and their activities and awareness of rabies (Marx, 1966; Verts and Storm, 1966; Hayne and Neeley, 1967; Constantine, 1967; and Sanderson, et al., 1967).

The primary wildlife hosts of rabies in the United States are foxes and skunks; these species accounted for 82 per cent of confirmed cases of rabies in wildlife in 1968. Unfortunately, rabies reports often do not distinguish between the two species of foxes and between the different species of skunks. Differences in epizootiology within these groups have not been clearly defined, but available information indicates that striped skunks more commonly support epizootics than do spotted skunks.

Raccoons and bats seem to be secondary hosts, but their role in perpetuating and spreading the disease is still not well understood.

Rabies has been sporadically observed in raccoons for some time and over a wide area of the United States. But the disease has reached near epizootic proportions only in Florida and southern Georgia. In 1968, 92 per cent of the rabid raccoons reported in the United States were from Georgia and Florida. Rabies was not reported in raccoons from Florida until 1947 (Scatterday, et al., 1960). Although there is no reason to doubt that the disease was previously present in raccoons, the rate of infection has apparently increased, and the disease has spread northward into southern Georgia where its advance has been marked by a well defined wave of reports. Davis and Wood reported in 1959 on hundreds of animals from southwestern Georgia examined for rabies. They found no rabid raccoons among 299 examined. Today rabid raccoons are commonly reported from that area.

Rabies in bats has long been recognized in the tropics, especially among the vampires. In the United States, rabies was first encountered in bats in 1953 in Florida (Scatterday, 1954). It has since been reported in bats from all of the 48 contiguous states, and the number of reported cases has steadily increased. But this increase in reported cases is prob-

ably due to increased public awareness, and there is no support for the popular idea that incidence has increased (Constantine, 1967).

Of the 40 native species of bats, at least 26 have been found to be infected (Constantine, 1967). Rates of infection in sample collections are usually about 1 per cent in resident bats and 3 per cent in migratory species (Constantine, 1967).

Geographic Patterns

Host species supporting epizootics of rabies differ from one region to another. The principal hosts south and east of the Ohio River are foxes; skunks are the major hosts in the Great Plains; and raccoons have been the primary hosts recently in Florida and southern Georgia. Although rabies may occur in foxes and skunks in the same area, epizootics and enzootics seem characteristically to be confined to one group or the other (Tierkel, 1959; Parker, 1962; Verts and Storm, 1966; Sanderson, et al., 1967; and Held, et al., 1967). This condition is apparently not entirely due to differences in density of host species. For example, Parker (1962) reported that populations of skunks in fox rabies areas were not appreciably lower than in skunk rabies areas, and fox populations were no less dense in skunk rabies areas than in fox rabies areas.

Apparently there are no substantial barriers to the spread of rabies between red and gray foxes. The number of rabid foxes in each species appears to be in proportion to their abundance in the area (Scott, 1955; Parker, et al., 1957; and Davis and Wood, 1959).

Rabies does not seem to spread readily from raccoons to other species, and geographic centers of fox rabies and raccoon rabies in Georgia and Florida have been generally distinct. Raccoon rabies has, however, spread into areas where fox rabies was already present, and there is currently some overlap.

Seasonal Patterns

Seasonal variations in incidence of rabies appear to be related to seasonal patterns of activity in the host species (migration, hibernation, breeding, parturition, and juvenile dispersal). Incidence of rabies among bats is higher in summer and fall when bats are most active (Richardson, et al., 1966, and Constantine, 1967). Rabies in foxes is reported more frequently during the breeding season (January and February) and during dispersal of young in the fall (Jennings, et al., 1960; Held, et al., 1967; and Lewis, 1968). Verts (1967) reported peaks in incidence of rabies in striped skunks during periods corresponding to breeding and reproduction.

FACTORS INVOLVED IN EPIZOOTIOLOGY

Modes of Transmission

The usual mode of transmission of rabies in nature is apparently the bite of rabid animals. But other modes of transmission are known.

Transmission of rabies virus by an air-borne medium has been demonstrated (Constantine, 1962). Two cave workers, who had entered a cave in Texas that was known to harbor rabid bats, contracted the disease without having been bitten. Carnivores were later caged in the cave in various types of cages designed to exclude bats and arthropods. The animals became infected and died of rabies (ibid.). Rabies virus was later isolated from the air of this cave (Winkler, 1968). Carnivores infected by airborne virus seemingly can spread the disease to other animals by the bite route (Constantine, 1966a). The airborne virus may be from the saliva or from the urine of bats. Rabies virus has been found in the kidneys of infected bats (Villa and Alvarez, 1963, and Constantine, et al., 1968b), and in the urine of bats (Girard, et al., 1965).

It has recently been demonstrated that carnivores can be infected by eating tissues of infected animals, with no mucosal lesions apparently necessary for transmission (Johnson, 1965; Soave, 1966; and Fischman

and Ward, 1968). Previous attempts at infecting animals by ingestion of the virus had been unsuccessful (Schoening, 1956, and Tierkel, 1959).

There is also evidence suggesting transmission through the milk of rabid animals to their offspring. The virus has been isolated from mammary glands (Johnson, 1965), and human deaths are alleged to have resulted from ingestion of milk from infected cows (Saulmon, 1966, and Fischman and Ward, 1968). Intra-uterine transmission has also been suggested, but there is evidence that the placenta is an effective barrier to transmission (see Johnson, 1965, and Verts, 1967, for references).

The epizootiological significance of the non-bite routes of transmission is presently unknown.

Behavior of Diseased Animals

The action of the rabies virus on the nervous system of infected animals causes changes in behavior that make possible the perpetuation of the disease by the unique route of biting.

The fearless, aggressive behavior of rabid animals facilitates spread of the virus in nature. It is probably significant that striped skunks and canines, which are most commonly involved in epizootic rabies, characteristically exhibit furiously aggressive behavior. By comparison, raccoons and certain other species that do not commonly support epizootics of rabies are often (but not always) benign and unaggressive when rabid. Scatterday, et al. (1960) referring to attacks on humans by rabid raccoons, wrote "if raccoons are no more aggressive toward each other than they were toward the victims interviewed in this study, it is difficult to understand how the infection can be maintained in the raccoon population."

Increased movement and wandering have long been associated with rabies. Rabid dogs commonly leave home and wander great distances. Increased movement is generally believed to be important in the perpetuation and spread of the disease. However, Parker (1962) noted that rabies in striped skunk populations appeared to be confined locally. Storm and Verts (1966) tracked the movements of a rabid striped skunk for 28 days prior to death using radio-telemetric methods. They reported, "Although the movements of the rabid skunk appeared to be somewhat aberrant during the last week of its life, they apparently were no more extensive than those of non-rabid skunks of the same sex and similar ages." They interpreted this as evidence supporting the hypothesis that rabies is maintained by local populations of striped skunks.

Host Density

Because of the method of transmission of rabies, it seems reasonable to assume that the rate of spread is related to the rate of contact between individuals of the host species which in turn is related to population density. That infection rates are related to host density is generally recognized (e. g., Moore, 1950; Wood, 1954; and Schoening, 1956). However, the extent to which rabies incidence is dependent upon host density has not been conclusively demonstrated and seems to vary with the host species.

Parker, et al. (1957) concluded that a high population density is necessary for an explosive epizootic among foxes, but a relatively sparse population can sustain an enzootic. Wood and Davis (1959) expressed the opinion that epizootic rabies depends upon many factors in addition to the number of foxes.

Among bats, one might suspect that colonial species would have higher incidences of rabies than non-colonial species because of the increased liklihood of contact. Evidence, however, indicates that this is not true. Schneider, et al. (1957) reported that of 5,503 bats examined for rabies in Florida, the rate of infection for non-colonial bats was seven times that for colonial bats. Richardson, et al. (1966) reported that in Georgia the rate of infection for non-colonial bats was ten

times that for colonial bats. The relationship of rabies to host density in bats is obscured, however, because most non-colonial bats are migratory and colonial forms are not.

Habitat Barriers

Ecological barriers often seem to limit the spread of rabies within a species. Parker, et al. (1957) observed that high fox population densities existed adjacent to enzootic regions and stated that it must be assumed that ecological barriers limit the spread. Jennings, et al. (1960) reported that an epizootic of fox rabies in northern Florida was largely restricted to 13 counties of red clay soils. Rivers, sandy soils and swamps did not support the epizootic. Apparently swamps and sandy soils did not support fox populations dense enough to sustain the epizootic.

It is apparent from reported cases of rabies (maps published annually by the National Communicable Disease Center) that large rivers commonly serve as partial barriers to the spread of epizootics. The spread of raccoon rabies in Georgia seems to have been arrested, at least temporarily, by the Chattahoochee River and the large reservoirs along it on the west and by the Altamaha River on the northeast. Counties to the east of the Chattahoochee River in southern Georgia have reported a high incidence of rabies in raccoons, while neighboring Alabama counties across the river have reported only one confirmed case of raccoon rabies from 1949 through 1968. Likewise the spread of an epizootic in foxes in central Tennessee and northern Alabama seems to be limited by the Tennessee River and impoundments along it.

Reservoir Species

Sporadic and enzootic rabies have presented the most vexing problems to public health workers. The disease must be supported either (1) by an inapparent, non-aggressive species, (2) at low levels by species periodically involved in epizootics, or (3) by a complex of species. Many investigators have expressed doubt that rabies virus can be maintained in non-epizootic form within a species by direct transmission from infected to non-infected individuals by biting. Some reasons stated by various workers are (1) it is known that a large percentage of individuals exposed to rabies do not become infected, (2) not all rabid individuals become infective, and (3) if rabid animals are only infective for a few days prior to death (as is generally assumed), the number of contacts with non-infected animals would be limited by low population density and behavioral isolation (e. g., clumped distribution, denning, and restricted movements in winter).

Because of these problems, many workers think that there must be some reservoiring mechanism by which the survival of the virus in infected individuals is prolonged (e.g., chronic, latent, or carrier rabies, prolonged incubation, etc.) and, perhaps, spread by non-bite routes (e. g., intra-uterine transmission and transmission to nursing young through the milk). There is much circumstantial evidence in support of some of these views.

Much of the remainder of this paper relates to certain aspects of the reservoir concept and the identification of reservoir species. It must be emphasized that it has not been proven that true reservoirs exist or that they are necessary to account for endemic and sporadic rabies in areas where population levels and other ecological factors allow transmission at a low rate.

Host Responses and Viral Characteristics

Chronic Rabies.—It is commonly assumed that rabies invariably terminates in death within a few days after symptoms appear, but this basic assumption has been questioned recently by several investigators. Bell (1966) suggested that rabies may occur in a "chronic" form characterized by one or more of the following: delayed onset, clinical recovery, clinical disease of long duration, or the healthy carrier state.

It has long been known that vampires may serve as true asymptomatic carriers of rabies in the tropics, and some researchers, especially in the Old World, have reported circumstantial evidence that terrestrial carnivores may serve as carriers (see Yurkovsky, 1962; Johnson, 1965; Bell, 1966; and Verts, 1967, for references). Cases have been reported of apparent recovery from rabies by dogs, spotted skunks, rodents and other animals (ibid.). Such cases have generally been regarded as curiosities, but some researchers now think that rabies may occur in forms other than the acute, lethal type more commonly than has been previously supposed. For example, Yurkovsky (1962) states ". . . the existence of rabies carriers is an indisputable, but insufficiently investigated fact." Experimental demonstration of chronic rabies has not been reported, however.

Latent Infections Re-activated under Stress.—It has been demonstrated that the rabies virus may remain latent in the tissues of an animal for long periods of time. Lapses of many months between exposure and onset of symptoms are not unusual, and a recent case of human rabies was attributed to exposure 22 months prior to the development of symptoms.

It has been shown that in bats brown adipose tissue (the "hybernating gland") stores the rabies virus during prolonged periods of latency (Sulkin, et al., 1959; Sulkin, 1962; and Allen, et al., 1964). The period of latency in bats is affected by metabolic rate, and incubation is suspended during hibernation (Sulkin, et al., 1960, and Sadler and Enright, 1959).

In other mammals a mechanism of latency has not been demonstrated, and the site of proliferation of the virus during long incubation periods is not known.

Limited evidence suggests that latent infections may be reactivated when the animal is placed under physiological stress, although controlled experiments have not been conducted. Guinea pigs and raccoons inoculated with rabies virus have developed the disease months later when subjected to a course of adrenocorticotropic hormone (ACTH) and (among guinea pigs) when subjected to crowded conditions (Soave, et al., 1961; Soave, 1962 and 1964; and Sanderson, et al., 1967). Secretion of ACTH is accelerated under conditions of social stress associated with high density populations (Christian, 1963).

Verts (1967) reported that peaks in incidence of rabies among striped skunks occurred when females were pregnant or lactating and that during this time reported cases of rabies were 15 times greater for females than for males. During the season of courtship and copulation reported cases were higher among males. Verts hypothesized that young skunks may acquire latent infections from an infected mother and that these latent infections may become reactivated in young males during the courtship period and in females during pregnancy as a result of added physiological stress (ibid.).

Sublethal, Immunizing Infections.—Recent investigations have provided evidence that sub-clinical immunizing infection occurs in wild animals in nature. Tierkel (1959) and Sikes (personal communication cited by Barr, 1963) report the presence of an antiviral substance from the serum of wild mammals. Serum samples from animals collected from several areas were tested for the presence of anti-viral substance (neutralization of at least 32 LD_{50} of rabies virus by undiluted serum). Among samples from areas with a history of recent fox rabies, tests were positive for the presence of antibodies in 4.6 per cent of 262 foxes, 5.6 per cent of 196 raccoons, 1.8 per cent of 185 opossums, 18.5 per cent of 27 bobcats, and 14.5 per cent of 48 skunks. All positive sera were from animals from epizootic and enzootic counties. Serum neutralization tests of nearly 300 animals from rabies-free areas were completely negative. In a survey in two counties in west central Florida in 1968, 10 of 43 raccoons had rabies antibodies (NCDC Annual Rabies Report—1968).

Sikes (1962) reported that several foxes and skunks inoculated with rabies virus developed serum rabies-neutralizing antibodies following inoculation. These animals never had clinical symptoms, and they survived a challenge dose of 16,000 MLD_{50} (median lethal dosage for mice) at the end of six months. Controls died from the challenge.

The epizootiological significance of rabies antibodies is not yet apparent.

Origin of Virus, Host Resistance and Ability to Transmit Virus.— Host-specific differences in susceptibility and ability to transmit virus and differences in invasiveness of viral strains may play an important role in preventing the spread of rabies from one species to another. Host species may differ in the amount of virus secreted, the amount of virus required for infection, natural resistance to infection, and in antibody formation after exposure.

The rabies virus can apparently be modified by repeated passage through the same host species, and different wildlife species may differ in susceptibility depending upon the source of the virus (Johnson, 1965). In experimental inoculations of foxes and skunks using virus isolated from fox salivary glands, Sikes (1962, 1966) found skunks to be 100 times more resistant to infection than foxes. Sikes noted that foxes secrete less virus in the saliva and require less for infection than do skunks. Parker and Wilsnack (1966), working with virus of skunk origin, were unable to demonstrate a significant difference in susceptibility of foxes and skunks. However, the incubation period was longer in skunks, and skunks shed more virus in the saliva.

Sikes and Tierkel (1961) found that raccoons were more resistant than foxes or skunks and secreted less virus. Opossums were highly resistant, and the investigators were unable to induce a fatal infection in opossums. Barr (1963) summarized studies of experimental infection of opossums with rabies. Although a small percentage of opossums were experimentally infected, some did not become infected even when subjected to doses of up to 634,000 MLD_{50} of street virus of skunk origin. Barr concluded that the opossum is highly resistant to rabies and that the mechanism involved is one of natural resistance rather than a naturally acquired immunity.

Constantine and associates (Constantine, 1966d, and Constantine, et al., 1968a) found that individual species of carnivores differ in susceptibility to rabies virus isolates from different species of bats, and that virus from an individual species of bat may differ in its capacity to infect different species of carnivores.

Sikes (1962, 1966) reported an interesting relationship between amount of inoculum and amount of virus in the salvia of infected animals. Foxes did not ordinarily secrete enough virus in the saliva to infect skunks, and foxes inoculated with quantities of virus comparable to the amount that would be received from the bite of a rabid skunk developed overwhelming infections and died before virus could multiply in the saliva (ibid.). This could provide a substantial barrier to the interspecific spread of rabies. However, it was reported that foxes receiving lesser amounts of inoculum (as might be received from the bite of a rabid fox) had longer incubation periods and nearly all emitted virus in the saliva (ibid.). The saliva of some contained enough virus to infect skunks, and Sikes indicated that where rabies occurred in fox populations for several years an eventual "spill-over" into skunks could be expected (ibid.). This conclusion is substantiated by reports from several areas.

POTENTIAL RESERVOIRS

Foxes

It is unlikely that rabies could persist undetected in fox populations for any substantial period of time. The disease is usually immediately apparent in foxes because of their high degree of susceptibility and aggressiveness when rabid. Johnson (1959, 1965) contends that rabies

occurs in canines when dense populations build up in regions where inapparent infections of rabies exist in other animals.

Skunks

Johnson (1959, 1965) believes that members of the mustelidae are permanent reservoirs throughout the world, and that the spotted skunk is an important reservoir in the United States. He cites as evidence the frequent sporadic reports of rabies in spotted skunks in areas where there is no evidence of the disease in other animals and the fact that spotted skunks are rarely involved in epizootics.

Verts (1967), however, pointed out that the spotted skunk does not occur in some areas where epizootics have occurred in striped skunks. He pointed out that the reservoir need not be a species that is not involved in epizootics and concluded that the striped skunk alone was responsible for maintaining rabies between epizootics during his study in Illinois. Epizootics were brought about by changes in the skunk population including but not restricted to changes in density.

Rodents

Tierkel (1958) stated that extensive surveys of small wild rodents have disproved suggestions that these species serve as reservoirs. Venters and Jennings (1962), reporting on the first record of rabies in a Florida rodent, stated that an estimated 3,000 sciurid rodents had been examined by the Florida State Board of Health without evidence of rabies infection. According to Winkler (1966), rodents account for 25 per cent of the heads submitted for rabies examination but contribute less than one half of 1 per cent to the total number of recorded rabies cases. Furthermore, "Experimental data reveals that most rodents are relatively refractory to infection with rabies and, even when infected with the disease, seldom are capable of shedding much virus in the saliva." (Ibid.)

Opossums

The opossum is extremely resistant to infection with rabies; few rabid opossums are reported, and serum surveys have revealed few reactors to serological tests (Barr, 1963; Sikes and Tierkel, 1961). It is unlikely that rabid wild opossums would transmit the disease to other wild animals by biting (Barr, 1963).

Raccoons

The role of raccoons in the maintenance and spread of rabies remains unclear, but it is doubtful if they are generally important reservoirs of rabies. Raccoons are somewhat resistant to the disease and generally secrete a relatively small amount of virus in the saliva (Sikes and Tierkel, 1961), and they are commonly not aggressive when rabid. Surveys have generally indicated a low rate of infection among raccoons, and, in areas of epizootic raccoon rabies in Georgia and Florida, the disease has been generally restricted to raccoons.

Bats

The ecology of rabies in bats is unclear, but bats are suspected reservoirs for rabies, and because they are highly mobile and may carry the virus for long periods of time, they have the potential to introduce the disease to rabies-free areas at great distances.

If bats do serve as an infective reservoir for the disease, it is not known how other animals might come into contact with them to become infected. Foxes and other carnivores might become infected by feeding upon moribund bats, either being bitten or becoming infected from ingesting infected tissue.

Frederickson and Thomas (1965), reporting on rabies in foxes in middle and eastern Tennessee, suspected that foxes were being reinfected through association with bats in caves. They reported an apparent relationship between the average number of rabid foxes reported by counties and the number of known caves in the counties. These data

were re-examined by Hayne and Neeley (1967), who concluded that the reported relationship was due to the method of presentation of th data.

It is by no means conclusively established that bats are important in the spread of rabies to other species. It has been definitely established that rabies can be transmitted from some species of bats to other mammals by biting, and several human deaths have resulted from rabies infections acquired from bites of bats (Bell, 1959; Constantine, 1966b, 1966c, 1967; and Constantine, et al., 1968a). However, it is not always easy to produce infection in other animals by subjecting them to the bite of bats (Tierkel, 1958; Burns, et al., 1958; Constantine, 1967; and Constantine, et al., 1968a). It was not until 1959 that this was accomplished experimentally (Bell, 1959), several unsuccessful attempts having previously been made (e.g., Burns, et al., 1958). Richardson, et al. (1966) wrote: "Bat rabies in Georgia has occurred predominantly in counties that were free of reported rabies in terrestrial mammals. . . . No epidemiologic evidence exists to date which suggests the transmission of rabies by bats to other animals in Georgia."

Constantine (1967) stated that the evidence suggests an independent virus cycle in bats with possible tangential transmission to carnivores. He emphasized that, because of behavioral and ecological and probable epidemiological differences, each species of bat must be considered separately.

As Hayne and Neeley (1967) have pointed out, biologists must treat this subject with restraint and responsibility, for the mind of the public is already filled with myths and superstitious dread where bats are concerned. Should the public come to associate bats with such a dreaded disease as rabies, fearful, misguided demands for bat control measures could easily result in extirpation of several especially vulnerable species.

SUMMARY AND CONCLUSIONS

Epizootics of sylvatic rabies in the United States are most commonly supported by foxes and striped skunks. In dense fox populations the disease spreads rapidly because of the high degree of susceptibility of foxes and because of the increased movement and furious behavior of rabid foxes.

Rabies is not readily transmitted from foxes to other species, probably because of lower susceptibility of other species, low rates of viral secretion by foxes, behavioral and ecological barriers, and possible differences in viral strains. Eventually, however, striped skunks become infected. Striped skunks are extremely aggressive when rabid, and the disease may or may not assume epizootic proportions. Sporadic cases occur in other more resistant and less aggressive species, but the disease rarely becomes epizootic.

Epizootics in fox populations usually terminate when host density is greatly reduced. Epizootics among striped skunks do not run their course as quickly because of greater host resistance and longer duration of infections.

Between epizootics rabies is perpetuated by one or more species that may vary from one area to another. Mechanisms maintaining the virus in individuals and in populations have not been satisfactorily demonstrated. Several theories supported by limited evidence have been offered including reservoiring in brown adipose tissue of bats during hibernation, latent infections and infections of long duration in carnivores, viral modification, host resistance, and acquired immunity.

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