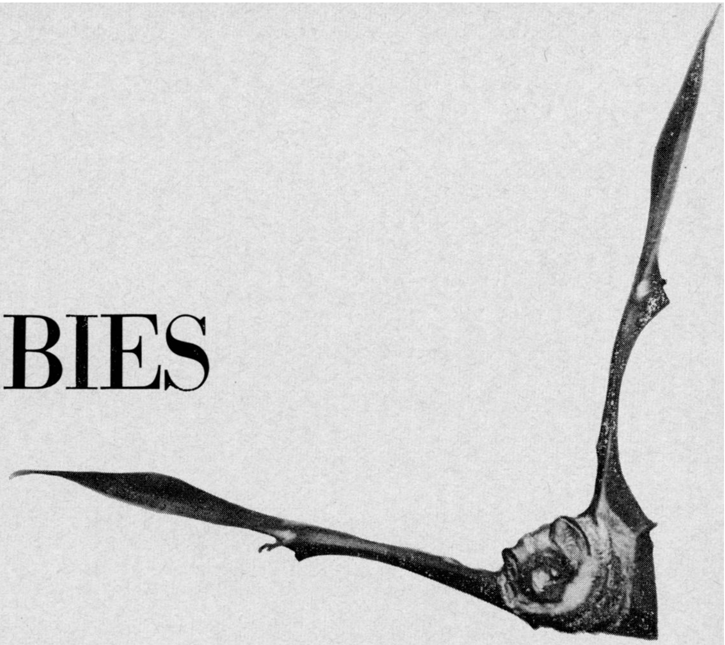
BAT RABIES in the SOUTHWESTERN UNITED STATES



DENNY G. CONSTANTINE, D.V.M., M.P.H.

BAT RABIES, first discovered in the United States in 1953 (*1*), has occurred throughout the country in at least 26 of the currently recognized 40 native bat species. Investigations of bat rabies in the Southwest by the Public Health Service's Communicable Disease Center began at Carlsbad, N. Mex., in 1956; after 1957, studies were centered at the Center's Southwest Rabies Investigations Station in University Park, N. Mex. Efforts were concentrated on the delineation of potentially dangerous species by determining susceptibility of various Carnivora to bat rabies virus when exposed by being bitten by infected bats, by intramuscular inoculations of virus, and by transmission of virus in air (*2–9*).

Other activities of the station provided data on infection rates, rabies morbidity, and non-rabies morbidity. Morbidity data resulted from surveys of rabies-suspect bats, many of which were tested by the station for health departments as a diagnostic service, although one State, California, made its reports available for this study (*10, 11*). Investigations of rabies-suspect bats yielded information on time and space distribution of morbidity in different bat species, exposures of man and animals to rabies-infected bats, behavior of infected bats, and distribution of virus in different bat tissues. Bizarre time and space patterns of morbidity were compared with patterns of bat activity for clarification. A new perspective of the epidemiology of the disease in bats resulted.

Dr. Constantine was formerly chief, Southwest Rabies Investigations Station of the National Communicable Disease Center, Public Health Service, at University Park, N. Mex. He is presently veterinary epidemiologist, Communicable Disease Center Activities, Naval Biological Laboratory, Naval Supply Center, Oakland, Calif. The photograph above was taken by the author.

Materials and Methods

Mouse inoculation tests, virus titrations, serum-virus neutralization tests, and fluorescent antibody (FA) tests were done by conventional techniques (*12*). Albino Swiss mice, about 3 weeks old, were used. Trituration of bat tissues was done with mortar, pestle, and abrasive agent. In 1958 the diluent used was 10 percent egg yolk, and in 1960, 0.75 percent solution of bovine albumin (Armour fraction V) was substituted for the egg yolk. Two milligrams of dihydrostreptomycin sulfate and 1,000 units of crystalline penicillin were included per milliliter of tissue suspension. Bat tissues comprised 10 percent, by weight, of suspensions, except for salivary gland tissues, which were 5 percent. Suspensions were centrifuged at 5° C. and 2,000 rpm for 10 minutes.

To collect saliva specimens from bats, the oral cavity was swabbed with cotton moistened with diluent. The cotton was rinsed in 0.5 milliliter of diluent, and the diluent tested for rabies virus by the mouse inoculation test.

Rabies mortality ratios reported for mouse inoculation tests were calculated by dividing the number of dead mice by the number of mice inoculated.

Data on bat morbidity were based primarily on numbers of rabies-virus infected bats found in Arizona, August 1959 to October 1963; Colorado, July 1959 to September 1963; and New Mexico, June 1958 to April 1964. Data on infected bats from California were derived from bats found from 1954 through 1965. Information from investigations on bat rabies virus infections at Carlsbad Cavern, N. Mex. (*8*), was omitted, except where specifically noted.

All rabies diagnoses reported in this paper were confirmed by serum-virus neutralization test or by FA test, because other viral agents which produce rabieslike deaths and inclusion bodies in inoculated mice have been found in bat tissues. Rio Bravo virus, frequently isolated in the United States from bat salivary glands (*13, 14*), has been present in bats whose salivary glands appeared rabies positive only by mouse inoculation test. Several isolations of Montana myotis leukoencephalitis virus (*15*) and Tacaribe virus (*16*) have been detected in brains and salivary glands of bats in the Western Hemisphere, where Kern Canyon virus in bat tissues has also been reported by Johnson, cited by Sulkin (*17*). Other viruses have been detected in bats in Africa (*18–22*). Exceptions to confirmation by serum-virus neutralization test or FA test are certain reports of positive mouse-inoculation tests using bat brain tissue only, but these are identified in the text.

The chi-square test for statistical significance was applied with the fourfold table method. The point biserial correlation coefficient was calculated in comparing weights of bat species and proportions of bat samples which bit man.

Results

Infection Rates

Significant data on rabies virus infection rates in clinically normal bats are relatively scarce, and information on seasonal differences is nearly nonexistent. Usually, many bats must be tested before an infected one can be found. Laboratory resources or availability of bats limited the number in samples of certain species from a few to several hundred, and infection rates detected in these samples generally varied from 0 to 3 percent. Data were from surveys or were obtained fortuitously as byproducts of other investigations.

In a survey to obtain rabies virus for experiments (*7*), saliva samples were collected from 150 clinically normal leaf-nosed bats, *Macrotus waterhousii*, held captive after capture in California in December 1958. One sample contained rabies virus. Conditions of captivity proved unsatisfactory for this species, and within a few days most bats had died, including the bat with virus in its saliva. Its brain also contained virus. These data provided evidence of a minimum infection rate of 0.67 percent. Saliva samples of 78 additional leaf-nosed bats, collected in California in March 1959, were negative for rabies. Dean and co-workers (*23*) reported that brains and salivary glands of 84 leaf-nosed bats collected in Arizona were negative for rabies virus infection in mouse inoculation tests.

One hundred (50 adults, 50 young) clinically normal cave myotis bats, *Myotis velifer*, collected in Frio Cave, Uvalde County, Tex., during July 1961 were negative, by mouse inoculation test, for rabies virus in brains, salivary glands, kidneys, and lungs (*9*). Dean and co-workers

(*23*) reported only positive mouse inoculation tests done on brains of two of 180 *M. velifer* tested in Arizona, a rabies infection rate of 1.1 percent in that sample.

One hundred clinically normal bats of the genus *Myotis* (15 *M. lucifugus*, 46 *M. yumanensis*, one *M. evotis*, seven *M. thysanodes*, 20 *M. volans*, and 11 *M. californicus*) collected during a survey in California (*24*) were negative for rabies virus by mouse inoculation test. Similar testing indicated 40 *Myotis* (26 *M. evotis*, 13 *M. thysanodes*, one *M. californicus*) from Arizona were negative for the virus (*23*).

Rabies tests on clinically normal bats of the genus *Myotis* from other sections of the United States produced similar results. In Montana, 83 *Myotis* (14 *M. yumanensis*, 47 *M. lucifugus*, 17 young of those two species, three *M. volans*, one *M. californicus*, and one *M. evotis*) were negative for the virus (*25*). Samples of *M. lucifugus* were reported rabies virus negative in Illinois, where 480 were tested (*26*), and in Massachusetts, where 83 were tested (*27*). However, Girard and co-workers (*28*) found two of 394, or 0.51 percent, asymptomatic *M. lucifugus* infected in New England. Schneider and co-workers (*29*) found rabies virus in one of 1,998, or 0.05 percent, *Myotis austroriparius* and in one of 281, or 0.4 percent, *Myotis grisescens* in Florida.

Asymptomatic silver-haired bats, *Lasionycteris noctivagans*, were negative for rabies virus infection. Seven were tested in New Mexico, one in California (*24*), and one in Massachusetts (*27*). Rabies was not detected in 10 western pipistrelles, *Pipistrellus hesperus*, in California (*24*) or in eastern pipistrelles, *Pipistrellus subflavus*, among 15 tested in Illinois (*26*) or 27 tested in Massachusetts (*27*). But two of 327, or 0.6 percent, of eastern pipistrelles tested in Florida were infected (*29*).

Dean and co-workers (*23*) obtained positive mouse inoculation tests only on brains of one of 52, or 1.9 percent, of big brown bats, *Eptesicus fuscus*, collected in Arizona. None of 36 additional big brown bats collected from a roost in Arizona in May 1961 was positive for rabies. Fifteen bats of this species tested in California (*24*), 37 in Montana (*25*), 40 in Illinois (*26*), and 138 in Massachusetts (*27*) were negative for rabies. However rabies was isolated from one of 63, or 1.6 percent, of asymptomatic bats in Ohio (*30*) and three of 119, or 2.5 percent, in New England (*28*).

Fifty hoary bats, *Lasiurus cinereus* (43 males, seven females), netted in flight in New Mexico and Arizona died in captivity before they could be used in experiments. One of the 50, a male, was infected with rabies virus. One netted in flight and four netted while resting in vegetation in California (*24, 31*) were negative to tests for virus. A female hoary bat netted while resting in vegetation in Iowa in August 1962 later died with rabies. Four females similarly collected in Iowa a year later (*32*) were negative to tests for the virus.

The 2 percent (1 of 50) infection rate demonstrated in apparently normal hoary bats collected in flight in New Mexico and Arizona is similar to findings for other species of the genus *Lasiurus*. Comparative data on the subject were acquired fortuitously from red bats, *Lasiurus borealis*, netted as they rested in vegetation in Iowa (*32*) and held captive for use in experiments (*6*). Of 44 red bats (18 males, 26 females) captured in August 1962, three males and one female died before experiment, which was started 41 to 45 days after capture. One male was infected with rabies virus, indicating the sample of 44 had a minimum infection rate of 2.3 percent. Fifty-five adult red bats (27 males, 28 females) captured in July and August 1963 died within 118 days of capture. None was infected. Twenty-one other adult red bats (10 males, 11 females) survived captivity and were started on experiment at that time. These data indicate that rabies virus infection in 1963 existed in less than 2 percent of red bats. Twenty red bats collected as they rested in trees in California were negative to tests for the virus (*24, 31*). In collections of lasiurine bats (*Lasiurus seminolus* and *Lasiurus intermedius floridanus* [*Dasypterus floridanus*]) in Florida (*29*), 1.1 percent of those collected in flight had rabies, compared with 0.8 to 1.2 percent of bats collected from vegetation (in the latter instance, a litter of three rabies-positive sucklings was considered as one bat).

Ninety-seven big-eared bats, *Plecotus townsendii*, were aroused from hibernation in a New Mexico cave in January 1959. Saliva samples were collected, and the bats were banded and replaced in the cave. One saliva sample produced illness in mice in the mouse inoculation test, but no agent was recovered in mouse passage or in subsequent saliva samples or tissues of the bat, which was recovered at the cave 2 months later. Twelve other big-eared bats were collected while in hibernation in two New Mexico mine tunnels in February and March 1961, and the bats were isolated in captivity. All died eventually; two with rabies, 77 and 80 days after capture. Clinically normal big-eared bats were negative for rabies virus, six in California (*24*) and 29 in Arizona (*23*).

Twenty-five pallid bats, *Antrozous pallidus*, collected in roosts in California were negative for rabies virus (*24*), and 31 big free-tailed bats, *Tadarida molossa*, netted in flight in New Mexico, were rabies virus negative (*33*).

Rabies virus usually was present in less than 1 percent of samples of clinically normal Mexican free-tailed bats, *Tadarida brasiliensis mexicana*, collected in New Mexico and Texas, although the infection rate evidently was as high as 3 percent in autumn (*8*, *34*). One of 12 collected in California was positive for the virus (*24*). Mouse inoculation tests of brain tissues of 86 bats in Arizona were positive for virus in two bats, or 2.3 percent (*23*). Four of 1,129, or 0.4 percent of southeastern free-tailed bats, *Tadarida brasiliensis cynocephala*, were infected (*29*).

To sum up the reports just cited, demonstrable rabies virus infection rates in bat genera usually considered to be residents (*Macrotus*, *Myotis*, *Pipistrellus*, *Plecotus*) generally were no greater than 1 percent, but rates in migratory genera (*Lasiurus* and *Tadarida*) were as great as 2 to 3 percent. An exception was *Eptesicus*, a resident, in which rates as high as 1.6 to 2.5 percent were detected.

Annual Morbidity

Numbers of bats infected with rabies virus detected in the United States increased steadily after the initial discovery of a rabid bat in 1953, and a similar increase was observed in California (table 1, fig. 1). Fewer data were available from Arizona, Colorado, and New Mexico (table 2), but they suggested a similar trend. However, no increase was evident in the percent of infected bats in annual samples of rabies-suspect bats in California; available data show that 12 percent (33 of 266 bats) tested prior to 1960 were infected with rabies virus, compared with 10.5 percent (49 of 465) in 1964 and 11 percent (72 of 653) in 1965.

A rise in percent of big brown bats infected with rabies virus (significant only at the 10 percent level, however) was observed in 1963 in combined data on suspect bats from Arizona, Colorado, and New Mexico (17 of 55 or 30.9 percent positive), compared with the previous 4

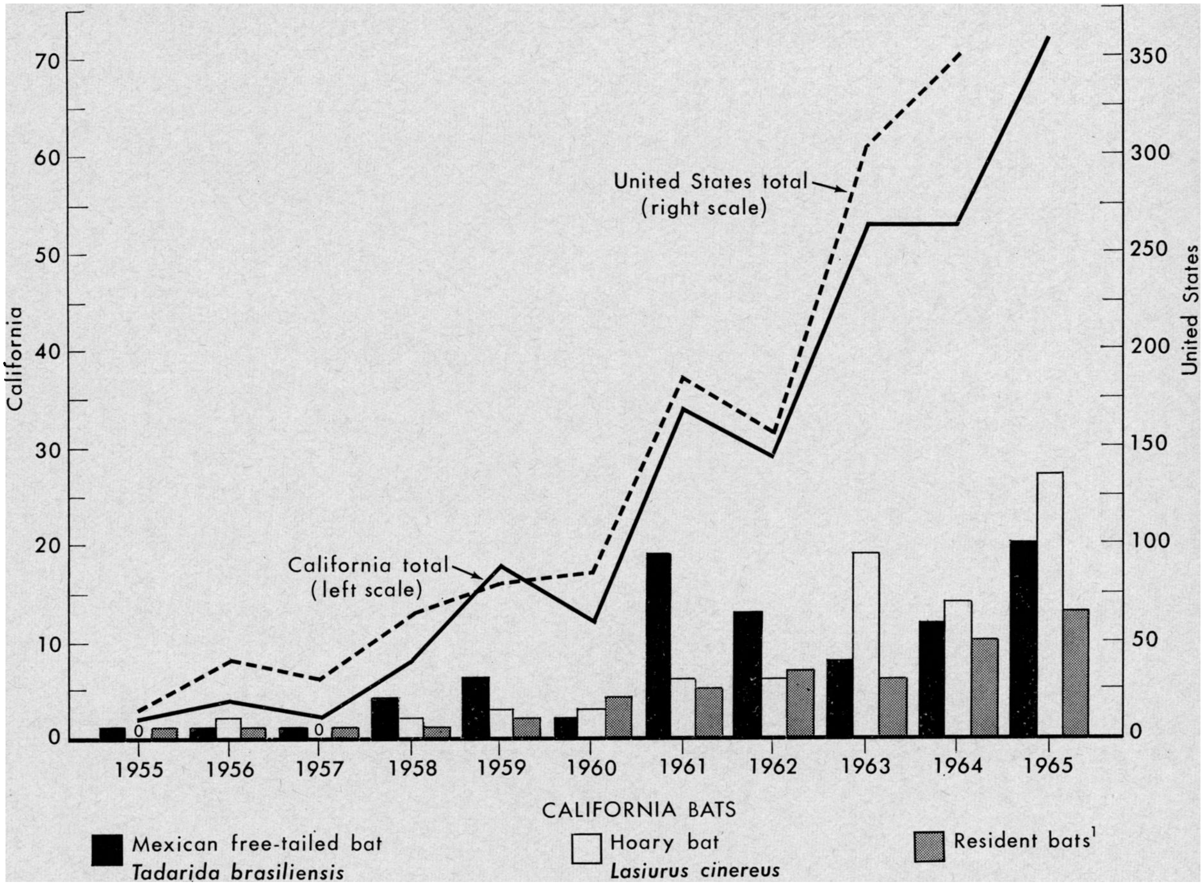
Table 1. Bats infected with rabies virus submitted in California, 1954–65

Species of bat	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965	Total
Leaf-nosed bat, *Macrotus waterhousii*					[1] 1								1
Yuma myotis, *Myotis yumanensis*								1			1		2
Long-eared myotis, *Myotis evotis*				1					1		1		3
Long-legged myotis, *Myotis volans*								1					1
California myotis, *Myotis californicus*		1						1	2			1	5
Small-footed myotis, *Myotis leibii*									1			2	3
Undetermined species of *Myotis*			1				1			3		4	9
Silver-haired bat, *Lasionycteris noctivagans*					1		1	2	1	3	3	2	13
Western pipistrelle, *Pipistrellus hesperus*						2	1				3		6
Big brown bat, *Eptesicus fuscus*							2	2	2	3	4	6	19
Red bat, *Lasiurus borealis*								1		1			2
Hoary bat, *Lasiurus cinereus*			2		2	3	3	6	6	19	14	27	82
Big-eared bat, *Plecotus townsendii*									1		1		2
Pallid bat, *Antrozous pallidus*						6					4		10
Mexican free-tailed bat, *Tadarida brasiliensis*	[1] 1	1	1	1	4	6	2	19	13	8	12	20	88
Species unknown						1	2	1	2	16	10	10	42
Total	1	2	4	2	8	18	12	34	29	53	53	72	288

[1] Bats exhibited no noticeable signs of disease when collected in surveys.

SOURCE: References 10 and 11.

Figure 1. Rabies-virus infected bats, California and the entire United States, by year, 1955–65



[1] Includes bats of the genera *Macrotus*, *Myotis*, *Pipistrellus*, *Eptesicus*, and *Plecotus*. Excludes *Lasionycteris*, *Antrozous*, and *Lasiurus borealis*, which appear to have migratory habits, at least in part, and unidentified bats.

years (five of 40 or 12.5 percent positive). However, no increase was evident in other bats during these periods, the 1963 percent being 15.7 (26 of 165) and the percent for 1958–62 being 15.6 (35 of 224). Peaks in annual incidence of cases in bats in California suggested that exceptional numbers of Mexican free-tailed bats died of rabies virus infection in 1961, and similar numbers of hoary bats died of rabies in 1963 (fig. 1).

It appears that outbreaks of rabies may have occurred in individual species, out of phase with one another, in California and other States. However, there may have been no real increase in rabies morbidity among all bats, since increases in submissions of rabies-virus infected bats were accompanied by like increases in submissions of bats free of rabies. Similarly, in Washington State, 14 percent (five of 35) of bats submitted in 1961 were infected, compared with 13.2 percent (31 of 234) submitted from January 1962 through July 1965 (personal communication dated August 6, 1965, from E. F. Baker, National Communicable Disease Center).

Seasonal Morbidity

It would have been preferable to relate data on rabies morbidity and nonrabies morbidity to relevant bat populations, but only general information on habits and abundance of bats was available. The majority of bat species are considered residents, although they shift to warmer shelters for winter (for example, *Macrotus*, which moves a few feet to several miles) or to cooler shelters to hibernate in winter (for example, the genera *Myotis*, *Pipistrellus*, *Eptesicus*, *Plecotus*, and in some instances *Lasio-*

nycteris and *Antrozous;* which move a few feet to 100 miles or more).

Other species (of the genera *Leptonycteris*, *Lasiurus*, *Tadarida*, *Eumops*, and in some instances *Lasionycteris* and *Antrozous*) appear to be migratory in varying degrees; in general, they winter in warm areas, usually south of the United States. Migrants occur in maximum abundance in the United States in summer, although in localities between summer and winter ranges they may appear only in spring and fall. Summer and early autumn are seasons of maximum bat activity in the United States, whether the bats are residents or migrants. Then young have been born and are growing rapidly, and all bats are accumulating fat for either hibernation or migration. Seasonal activity was reflected by numbers of rabies-infected or rabies-suspect bats received in California (fig. 2), Colorado, New Mexico, and Arizona (fig. 3), although the latter two States received relatively greater proportions of transient migrants in spring and fall. The season of bat activity evidently shortens as summer shortens according to latitude.

Rates of infection in suspect bats, cited subsequently, were derived only from data from Arizona, Colorado, and New Mexico, because in California species determinations were not made on bats negative for rabies virus. In addition, data from California did not include information on age and sex of bats.

Hoary bats were found in a time and space pattern (figs. 2 and 4) consistent with Findley's description of the habits of the species (*35*). They were noted in Arizona and New Mexico in spring, when the northbound migration was in progress, and in autumn during the southbound migration. The majority taken in Colorado were collected when they were in summer

Table 2. Results of tests for rabies virus in suspect bats from Arizona, New Mexico, and Colorado [1]

Species of bat	Bats tested by State of origin			Rabies-infected bats
	Arizona	New Mexico	Colorado	
Leaf-nosed bat, *Macrotus waterhousii*	1	0	0	0
Long-nosed bat, *Leptonycteris sanborni*	2	0	0	0
Little brown myotis, *Myotis lucifugus*	0	0	1	0
Yuma myotis, *Myotis yumanensis*	7	1	1	0
Cave myotis, *Myotis velifer*	16	0	0	0
Arizona myotis, *Myotis occultus*	2	0	0	0
Long-eared myotis, *Myotis evotis*	2	0	3	0
Fringed myotis, *Myotis thysanodes*	1	0	0	0
Long-legged myotis, *Myotis volans*	1	4	7	0
California myotis, *Myotis californicus*	3	1	0	0
Small-footed myotis, *Myotis leibii*	5	5	2	2
Silver-haired bat, *Lasionycteris noctivagans*	5	3	6	3
Western pipistrelle, *Pipistrellus hesperus*	13	0	0	9
Big brown bat, *Eptesicus fuscus*	47	3	40	22
Hoary bat, *Lasiurus cinereus*	31	8	18	20
Southern yellow bat, *Lasiurus ega*	8	0	0	0
Spotted bat, *Euderma maculatum*	0	[2] 2	0	0
Big-eared bat, *Plecotus townsendii*	2	0	1	1
Pallid bat, *Antrozous pallidus*	10	27	0	3
Mexican free-tailed bat, *Tadarida brasiliensis*	127	70	0	24
Pocketed free-tailed bat, *Tadarida femorosacca*	1	0	0	0
Big free-tailed bat, *Tadarida molossa*	0	8	1	1
Western mastiff bat, *Eumops perotis*	3	0	0	0
Underwood's mastiff bat, *Eumops underwoodi*	[2] 1	0	0	0
Total	288	132	80	85

[1] Bats were collected as follows: Arizona, August 1959–October 1963; New Mexico, June 1958–April 1964; Colorado, July 1959–September 1963.

[2] These 3 bats exhibited no signs of illness when collected in surveys but died with signs of disease after successful adaptation to captivity.

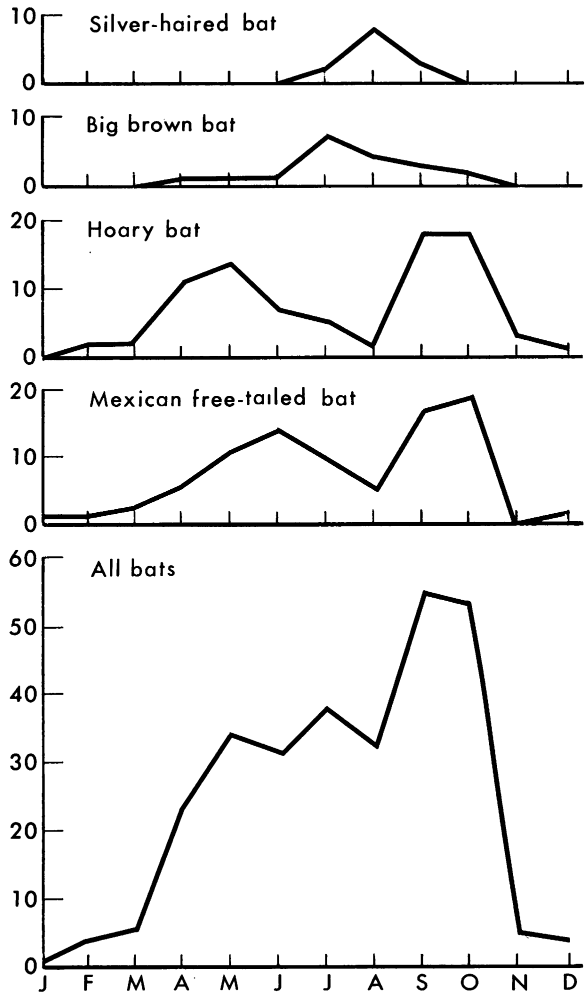
habitat. The overall rabies infection rate in combined samples of bats from Arizona, Colorado, and New Mexico was 35.1 percent (20 of 57). Seasonal rates were March through May, 14.3 percent (one of seven); June and July, 46.2 percent (six of 13); August through November, 35.2 percent (13 of 37). The highest rate was observed in summer, although the greatest numbers of infected bats were found in autumn. Infection rates were similar for both sexes; females, 33.3 percent (nine of 27) and males, 36.7 percent (11 of 30). Rates appeared higher in identifiable adults (44 percent or 14 of 32) than in bats identifiable as immature (one of six), but a greater proportion of young bats would be expected to be downed by accidents, accounting for the difference.

Big brown bats are generally considered a resident species rather than migrant, although their habits in the western United States have not been completely studied. Discovery of downed bats of this species was unimodal in time, peaking during warm months, when numbers of bats and bat activity should have been greatest for a resident species (figs. 2 and 4). The rabies infection rate in suspect big brown bats was 24.5 percent (22 of 90). The rate appeared relatively low in January and May (one of 11 or 9.1 percent), but it was high in June through July (nine of 42 or 21.4 percent) and in August through September (12 of 38 or 31.6 percent). Rates were similar for both sexes, females 25.0 percent (14 of 56) and males 24.2 percent (eight of 33). In bats identifiable by age, rates were 27.1 percent (13 of 48) in adults and 20 percent (seven of 35) in immature bats.

Suspect silver-haired bats were submitted in the spring and autumn in Arizona and New Mexico but in the summer in Colorado. The total sample received from these States was small, but 21.4 percent (three of 14) were positive to tests for rabies. The seasonal occurrence of rabies-virus infected silver-haired bats in California was unimodal (fig. 2), similar to bats received from Colorado.

Pipistrelle bats, although few in number, were found in nonwinter months and in unimodal distribution, as expected in this resident species. The overall rabies infection rate in the sample from Arizona (table 2) was 69 percent (nine of 13). All infected bats were females, in which

Figure 2. Submissions of bats with rabies virus, California, by month, 1954–65



the rate was 90 percent (nine of 10). Bats whose age could be determined included four adult females, three adult males, and two immature females.

Mexican free-tailed bats were picked up in a space and time pattern consistent with the habits of the species (figs. 2 and 4). Many were found in spring during the northbound migration, and greater numbers were found during the autumnal southbound migration. Rabies virus infections in specimens from Arizona and New Mexico were detected in 12.2 percent (24 of 197). Seasonal rates were January through May, 17.8 percent (five of 27); June and July, 44.9 percent (four of nine); August through October, 9.4 percent (15 of 160). The highest rate was in summer, but greatest numbers of infected bats were found in autumn. Infection rates were similar by sex; females 12.8 percent (15 of 117) and males 9.2 percent (seven of 76). Bats identified as adults had a higher rate (12 of 74 or 16.2 percent) than immature bats (three of 45, or 6.7 percent).

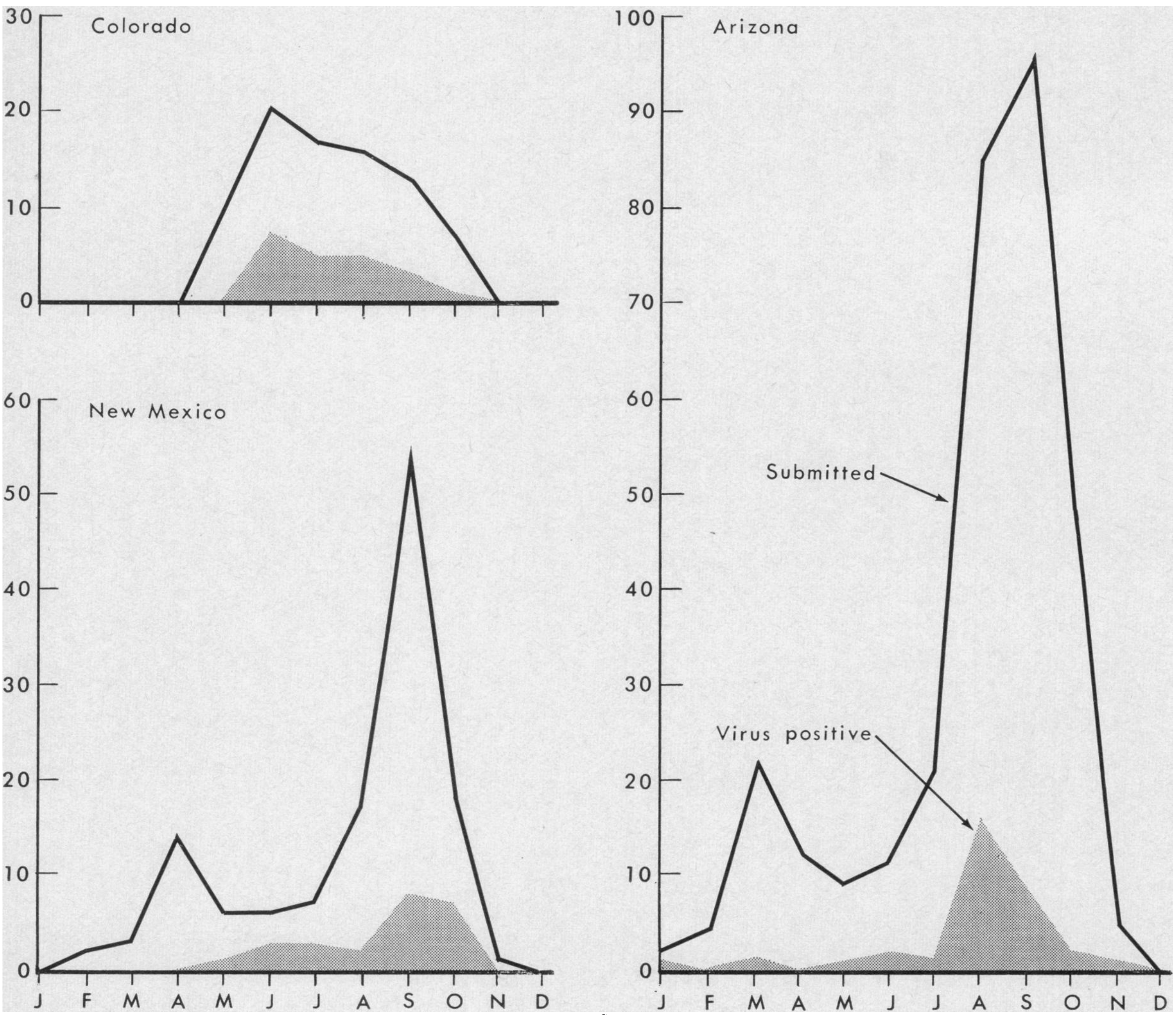
Signs of Morbidity and Exposures

Of rabies-virus infected bats with pertinent histories of signs, an average of 90 percent were alive when first observed, with the percentage varying from 83 to 100 among different genera (table 3). Twelve percent of the live bats were in flight; at least 64 percent were obviously ill or paralyzed. Greater proportions of silver-haired bats and Mexican free-tailed bats were observed flying than proportions of live bats of other genera (statistically significant at 2 percent for the silver-haired bat and at 10 percent for the Mexican free-tailed bat).

Eighty-seven contacts with persons and 111 contacts with pets occurred during discovery of 373 rabies-virus infected bats (table 3). Thirty-nine persons were bitten among the total of 275 live infected bats found, a ratio of 14.2 bites per 100 live bats. One person died from rabies after being bitten (*36, 37*). Antirabies treatment was administered in cases where information on treatment was available, but the information was not generally available. The pets, 39 dogs and 72 cats, were known to have experienced bat bites in certain instances, but usually this fact was not known.

Rates with which infected bats bit man de-

Figure 3. All submissions of bats suspected of having rabies, by month



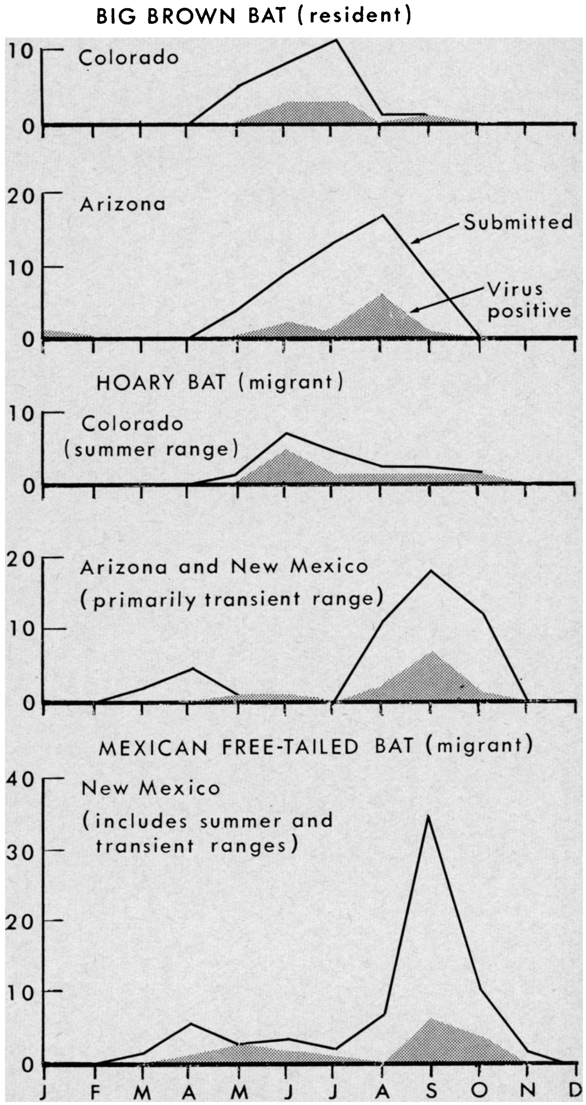
creased as bat weight in grams increased. They were *Pipistrellus*, 66.6 percent; *Myotis* and *Lasionycteris*, 30.4 percent; *Eptesicus*, 15.4 percent; and all other identified genera, 6.7 percent. The point biserial correlation coefficient between bat species weight and the proportion biting man for 232 recorded cases (those in which live bats were discovered and identified at least to genus) was $r = -0.34$. This value is significantly different from zero ($\chi^2 = 30.9$ with 1 degree of freedom, $P < 0.00001$). There were no significant differences in frequencies with which pets were found with infected bats of different genera or sizes.

Most bites occurred when persons either deliberately handled partially paralyzed bats or accidentally came into contact with them. Few persons were bitten by flying bats. Fewer bites were clearly unprovoked attacks. Whether bites were provoked may be inconsequential after the bite has occurred, but the distinction appears significant in understanding the nature of the hazard to man. Bats usually had signs of paralysis; some exhibited signs of depression which progressed to lethargy and hypothermia. Depression sometimes was preceded or replaced by evidence of discomfort or unusual belligerence; species which ordinarily avoid detection by remaining motionless and quiet moved about and squeaked, particularly when approached by an intruder. Partially paralyzed bats sometimes thrashed about on the ground, alternating between efforts to fly and efforts to bite nearby objects. Self-mutilation was uncommon. Bats with signs of rabies generally appeared concerned only with their own discomfort. They seemed to lack the intent to attack man deliberately, and their ability to do so was restricted.

Indisputably unprovoked attacks by bats infected with rabies appeared to be rare. Evidently at least two of the 227 live, infected bats discovered in California engaged in such attacks; two attacks were reported in Arizona, and one in Montana (*38*). An unidentified bat, thought to have been of the genus *Myotis*, flew into a patio in California at 5:30 p.m. and bit a boy behind one ear. One California myotis repeatedly landed on the clothing of a person in Montana and chewed it. A small-footed myotis, released just after capture in Arizona, flew away but soon returned to bite an observer; the bat ferociously bit fabric placed in the receptacle in which it was housed before it died. A western pipistrelle repeatedly attacked two men in a mine near Death Valley, Calif. Another pipistrelle bit at the shoe of a person sitting at a picnic table in Arizona.

Other attacks cannot be readily differentiated from altered flight ability or disorientation of the diseased bat. Apparently these bats blunder into obstacles instead of avoiding them, and they may fly in the daytime and into unusual places, apparently for shade. Airborne bats, experiencing failing flight capabilities, do not differ from normal bats in their preferences for

Figure 4. Submissions of three species of bats suspected of having rabies, by month



elevated landing sites; they alight in unusual sites rather than on the ground, and a conveniently positioned person may suffice. I have been circled by nonrabid bats with flight impediments; they avoided me until ground contact seemed imminent and then landed on my clothing. It appears that bats may come in contact with man either as an obstacle or as a refuge. The disoriented rabies-infected bat may bite to avoid falling from an elevated landing site, or as an aid in climbing, a habit of normal hoary bats. A person on whom a bat has landed tends to brush it off, a procedure that elicits bites, whether or not the bat has rabies.

Hoary bats infected with rabies have been observed flying against inanimate and animate objects. One struck a tree trunk in Montana and fell to earth (*25*). Another, observed flying in New Mexico at noon, struck a tree limb and fell into a pond. Still another struck a "mist net," erected at a New Mexico waterhole to snare drinking bats; the bat and a companion of the same species fell from the net into the water. The companion flew away, but the infected bat flew into the net a second time and was captured. At midday in New Mexico an infected hoary bat circled playing children and gradually lost elevation; finally it lighted on a child's back and bit at her clothing. Another hoary bat landed on a child's clothing in California, but no bite was reported. Still another "swooped down" from a tree in California, bit a child on the chest, fell to earth, and died. An infected hoary bat, flying in daylight, landed on a child in a doorway in Arizona; the child was bitten on his hand.

Similar behavior has been observed in other species. In California, a big brown bat infected

Table 3. Clinical state of rabies-virus infected bats when found and contacts of bats with persons and pets, Arizona, California, Colorado, and New Mexico [1]

Bat species	Clinical condition of bats						Contacts with bats				
	Alive						Man		Pets [2]		
	Partially paralyzed	Miscellaneous	Flying	Dead	Not reported	Total bats	Bite	Nonbite [3]	Dog	Cat	Total contacts
Leaf-nosed bat	0	1	0	0	0	1	0	0	0	0	0
Yuma myotis	1	1	0	0	1	3	0	0	0	2	2
Long-eared myotis	2	0	0	0	0	2	2	0	0	0	2
Long-legged myotis	1	0	0	0	0	1	1	0	0	0	1
California myotis	3	1	0	1	0	5	0	1	0	0	1
Small-footed myotis	3	2	0	0	0	5	3	0	0	2	5
Myotis, species undetermined	4	1	0	1	2	8	0	1	1	2	4
Silver-haired bat	5	4	5	1	1	16	4	1	2	3	10
Western pipistrelle	5	4	0	1	4	14	6	2	0	2	10
Big brown bat	14	10	2	2	13	41	4	3	4	9	20
Red bat	0	0	1	0	1	2	1	0	1	1	3
Hoary bat	55	14	7	8	15	99	4	26	13	20	63
Big-eared bat	2	1	0	0	0	3	0	0	0	1	1
Pallid bat	9	3	1	0	0	13	1	3	2	4	10
Mexican free-tailed bat	43	16	11	14	22	106	5	9	10	15	39
Big free-tailed bat	0	0	0	0	1	1	0	0	0	0	0
Species undetermined	30	7	6	2	8	53	8	2	6	11	27
Total	177	65	33	30	68	373	39	48	39	72	198

[1] Bats were found as follows: Arizona, August 1959–October 1963; California, September 1954–December 1965; Colorado, July 1959–September 1963; New Mexico, June 1958–April 1964.

[2] Although some pets were bitten, in most instances pets were observed with bats in their mouths or playing with bats.

[3] The majority of nonbite contacts consisted of deliberate handling of bats.

with rabies landed on the back of a child, then flew to a dog. In the same State, three infected Mexican free-tailed bats flew into obstacles; one flew into a wall, another a bench, and a third against a door.

Pathogenesis of Infections in Bats

Bats were captured routinely and kept in individual cages before and during use in various studies at the Southwest Rabies Investigations Station. Bats which died while being held were tested; some were infected with rabies virus. Data were collected on disease incubation periods, distribution of virus in different tissues, overwintering of the virus, appearance and disappearance of virus in saliva, and nature and duration of rabies signs. Additional data were derived from suspect bats, bats taken in surveys, and bats infected with the virus in experiments.

A female leaf-nosed bat, captured in a mine tunnel in California on December 30, 1958, had no signs of rabies at capture, but its saliva contained virus. It died after several days in captivity, but many other bats of the same species also died, apparently of causes other than rabies. Rabies virus was isolated from the brain of the one bat, but its salivary glands were negative for the virus by mouse inoculation test.

Two big-eared bats, collected March 13, 1961, while hibernating in mine tunnels in New Mexico, died in captivity, the adult male after 80 days and the adult female after 77 days. These bats had been kept active in a warm environment since capture. No signs of disease were observed before death. Saliva specimens, collected June 1, 1961, were negative for virus by mouse inoculation tests. Rabies virus was isolated from the brains of both bats and from the salivary glands of the male.

A male red bat, collected at rest in vegetation in Iowa on August 6, 1962, died 24 days later, after 4 days of irritability. The bat did not eat all of its food the day before it died. Rabies virus was detected in its brain and salivary glands.

An adult female hoary bat was discovered by its squeaking as it rested in full sunlight on an elm tree in Las Cruces, N. Mex., on September 17, 1959. Samples of its saliva were positive for rabies virus on the fifth day after capture but negative on the sixth day. The bat died on the ninth day, and rabies virus was isolated from its brain, but was not detected by mouse inoculation test in its salivary glands.

A male hoary bat, netted October 7, 1959, as it attempted to drink in flight at a pond in New Mexico, was found dead in its cage 17 days later. Rabies virus was isolated from its brain, but its salivary glands were negative for the virus by mouse inoculation test.

An adult female hoary bat, captured August 3, 1962, as it rested on a tree in Iowa, died 31 days later after 4 days of partial anorexia. Rabies virus was isolated from its brain, but its salivary glands were positive for the virus only by FA test.

Of hundreds of Mexican free-tailed bats held captive in a warm environment, five died of rabies after periods of 7, 20, 31, 85, and 90 days. They showed disease signs varying from anorexia and ataxia to paralysis for 1 to 2 days. Brains of the five bats were positive to tests for rabies virus by mouse inoculation and by FA test, but the salivary glands were negative in these tests except for two bats whose salivary glands were positive only by FA test (*34*).

Generally, bats with signs of rabies when first observed either were killed by the discoverer or died after a brief period. Signs usually were reported by excited discoverers after short observation periods, and interpretation of signs varied. Available information on the subject has been presented in the "Signs of Morbidity and Exposures" section.

Rabies virus was present in the brains of all infected bats, but it was not always detected in salivary glands (tables 4 and 5). Virus was isolated from other tissues of some infected bats. One of two western pipistrelle bats had virus in its lung tissues, but no virus was detected in their kidney, adrenal, or brown fat tissues. Tissues of big brown bats similarly tested contained rabies virus as follows: lungs, three of eight bats tested; kidneys, one of eight; adrenals, two of eight; brown fat, three of nine. A red bat was negative to tests for virus in these tissues, but one of seven rabies-positive hoary bats contained the virus in all of these tissues.

Throughout July 1962, many partially paralyzed or recently dead Mexican free-tailed bats were collected from caves in Texas. Rabies virus was detected in tissues of 130 of the bats as follows: brains 100 percent, salivary glands

78.5 percent, lungs 30 percent, and kidneys 11.5 percent. In further tests on 50 of the 130 bats, brown fat of two contained rabies virus, but all were negative to tests for virus in liver, spleen, pectoral muscle, intestine, and fecal pellets (*9*).

Bats experimentally infected with autogenous rabies virus showed noteworthy responses (*3–8*). Frequently a great proportion of bats infected by intracranial inoculation of virus developed signs of furious rabies in contrast to few or no signs in bats infected intramuscularly or to captive, naturally infected bats. The mortality rates were 71 to 100 percent following intracranial inoculation compared with rates of 13 to 25 percent produced by the intramuscular route. Deaths usually occurred 14 to 37 days after inoculation, but a Mexican free-tailed bat inoculated by intracranial route died 57 days later, and a red bat inoculated intramuscularly died 145 days later. Another Mexican free-tailed bat infected by intracranial inoculation died 108 days later; however, rabies virus could be detected only by FA tests and only in its salivary glands.

Inactivation of virus in salivary glands before death evidently occurred in certain naturally infected bats (leaf-nosed bat, hoary bat, Mexican free-tailed bat) and in experiments using certain species (big brown bat, hoary bat, red bat). Virus inactivation evidently occurred in the brains of certain bats inoculated intracranially; some did not develop discernible signs of disease, and others developed signs of disease but returned to normal (silver-haired bat, red bat, Mexican free-tailed bat). Still others survived with sequelae. A Mexican free-tailed bat, which had rabies signs 28 days after inoculation, survived with signs for 76 days; rabies virus was not detected in its brain at death, but virus was detected by FA test in its salivary glands, although the glands were negative for virus by mouse inoculation test. Six Mexican free-tailed bats were killed 181 days after intracranial inoculation of virus, when all but one bat had returned to normal health after exhibiting rabies signs; rabies virus was not detected in their tissues.

Characteristics of Virus from Bats

Mice that were inoculated intracranially with tissue suspensions from naturally infected bats exhibited periods of incubation and illness which generally were consistent in duration

Table 4. Responses of laboratory test mice to intracerebral inoculations of suspensions of brain tissues of bats naturally infected with rabies

Bat species arranged phylogenetically	Mouse inoculation tests						Titrations		
	Number of bat brains represented	Days before death		Days ill		Mouse mortality (percent)	Number of virus isolates titered	Titer [1]	
		Range	Mean	Range	Mean			Range	Mean
Leaf-nosed bat	1	6–11	9.5	0–0	0	100	1	------------	4.83
Small-footed myotis	2	14–15	14.5	0–1	.75	100	1	N.D	3.40
Silver-haired bat	[2] 3	10–19	15.8	0–5	1.50	100	1	do	3.17
Western pipistrelle bat	[2] 4	8–23	14.5	0–7	1.49	88	1	do	<2.0
Big brown bat	[2] 19	9–17	12.8	0–3	1.08	100	7	2.6–4.5	3.58
Red bat	5	13–21	16.8	0–3	1.18	100	5	2.5–4.8	3.25
Hoary bat	22	6–20	14.1	0–11	1.83	98	14	2.5–4.7	3.56
Big-eared bat	3	11–15	13.0	0–3	1.50	100	1	N.D	1.67
Pallid bat	[2] 1	13–15	14.3	0–1	.66	100	1	do	2.25
Mexican free-tailed bat	30	4–17	7.6	0–5	.65	98	1	do	2.83
Do	---------	---------	-----	---------	------	---------	[3] 25	0.7–7.2	3.70
Big free-tailed bat	1	13–18	15.2	0–3	1.50	100	0	------------	------

[1] Numbers of 50 percent mouse lethal doses per 0.03 gram of bat tissue, given as exponent of 10.

[2] Rabies was detected by fluorescent antibody technique in brain tissues of these additional bats, but mice did not succumb following intracerebral inoculation of tissue suspensions: 1 silver-haired bat, 1 pipistrelle bat, 2 big brown bats, 1 pallid bat.

[3] From Carlsbad Caverns, N. Mex., and Texas.

Note: N.D.—not done.

Table 5. Responses of laboratory test mice to intracerebral inoculations of suspensions of salivary gland tissues of bats naturally infected with rabies

Bat species arranged phylogenetically	Mouse inoculation tests		Titrations		
	Number of bat salivary gland sets represented	Mouse mortality (percent)	Number of bat salivary gland sets titered	Titer [1]	
				Range	Mean
Silver-haired bat	[2] 1	80	0		
Western pipistrelle bat	[2] 1	100	0		
Big brown bat	[2] 12	91	4	<1. 3–4. 3	2. 70
Red bat	4	73	2	3. 1–5. 8	4. 45
Hoary bat	15	73	6	1. 3–5. 5	4. 2
Big-eared bat	1	100	0		
Pallid bat	(2)				
Mexican free-tailed bat	[2] 14	93	0		
Do			[3] 6	1. 3–4. 3	2. 8
Big free-tailed bat	1	50	0		

[1] Numbers of 50 percent mouse lethal doses per 0.03 gram of bat tissue, given as exponent of 10.
[2] Rabies was detected by fluorescent antibody technique in salivary gland tissues of these additional bats, but mice did not succumb following intracerebral inoculation of tissue suspensions: 1 silver-haired bat, 2 pipistrelle bats, 3 big brown bats, 2 pallid bats, and 3 Mexican free-tailed bats.
[3] From Carlsbad Caverns, N. Mex., and Texas.

among mice when inoculums were from a single species of bat. Interesting differences and similarities in these periods were observed between mice given inoculums from different species of bats (tables 4 and 5).

The period from inoculation to death was exceptionally short in mice inoculated with virus from the Mexican free-tailed bat, and the period of illness also was brief. These results do not differ from those of other workers (*39–43*). Results closely corresponding to experiments with the free-tailed bat were observed when virus from the leaf-nosed bat was inoculated. These two species are members of the families Molossidae and Phyllostomidae, families which are primarily tropical in distribution. Silva and coworkers (*44*) reported similar results with rabies virus from the leaf-nosed bat, *Phyllostomus hastatus*, in Brazil. Tellez Giron (*45*) reported like results with rabies virus from the vampire bat, *Desmodus rotundus*, in Mexico; however, Johnson (*46*) reported somewhat longer periods before death. The periods of incubation and illness were longer for mice inoculated with rabies virus from the big free-tailed bat, an uncommon molossid found from South America to Canada.

The remainder of the rabies virus isolates tested in this study were from bats of the family Vespertilionidae, primarily temperate and subtropical in distribution. These isolates produced longer incubation periods and longer periods of illness in mice than those produced by isolates from Molossidae and Phyllostomidae. Similar long periods were reported by other workers in tests with rabies virus from bats of the vespertilionine genera *Myotis* (*38*), *Eptesicus* (*30*, *47*, *48*), *Dasypterus* (*49*), and *Lasiurus* (*49*).

Although rabies virus from any given species of bat generally produced remarkably uniform responses in mice, an outstanding exception occurred in rabies from the pallid bat. Mice inoculated with virus from a bat from New Mexico had incubation periods of 13–15 days, compared with periods of 18–34 days in mice inoculated with virus from a pallid bat collected in California. In contrast, rabies viruses from red bats found in Georgia, Iowa, and Texas produced incubation periods in mice distributed uniformly between 13 and 21 days.

Comparison of titers of rabies virus as the virus occurred naturally in salivary glands and brains of individual symptomatic bats indicated that virus in salivary glands had a higher titer than that in the brain in one of six Mexican free-tailed bats, two of four big brown bats, four of five hoary bats, and in one red bat. These samples were biased in favor of detecting higher titering virus isolates in salivary glands, because titrations were not attempted on virus inoculums which had not killed all mice in mouse inoculation tests. This interpretation is supported by the lower mortality ratio generally observed in mice inoculated with virus in salivary gland suspension (tables 4 and 5), a rate still lower if one includes salivary glands containing virus detectable only by FA test. This development may reflect a lowering of the level of virus activity in salivary glands before death.

This phenomenon was evident in some bats experimentally infected with rabies (*6*, *7*), and it occurred in naturally infected captive bats mentioned previously. However, higher titering viruses were not as readily found in salivary glands of the Mexican free-tailed bat, a molossid, as they were found in the vespertilionid bats. Bell reported detection of higher titers of rabies virus in salivary glands of some vespertilionid bats (*47*).

Examinations for Negri bodies were not done routinely, because the more reliable serologic techniques were employed for virus identifications. However, Negri bodies were observed in brains of individual specimens of all bat species or in brains of first-passage mice.

Data in tables 4 and 5 on responses of mice to intracerebral inoculations of bat rabies viruses and data on responses of certain Carnivora to intramuscular inoculations of bat rabies viruses (*4*, *6*, *7*) were summarized and arranged in an order indicating the degree in which the bat species from which the viruses originated associate with other species and with each other (tables 6 and 7). Degrees and frequencies of interspecific and intraspecific host associations were estimated from observations on geographic, ecologic, and social distributions of the various species when in roosts, foraging, or during migration; associations varied greatly by place, time, and abundance of bats. Intraspecific gregariousness appeared important because of implications concerning natural methods of transmission (bite or airborne, *2*, *4*, *6*) and passage rate. Interspecific association appeared important for the same reasons and also because of implications concerning differentiation of virus within each species. The degree of differentiation of virus within a given host species should be influenced by the degree and duration of

Table 6. Responses of laboratory test mice to inoculations of tissue suspensions from bats infected with rabies

Bat species origin of inoculum [1]	Natural gregariousness of species [2]	Highest virus titers detected [3]		Mice inoculated by intracerebral route [4]	
		Bat brain	Bat salivary gland	Days before death (mean)	Days ill (mean)
Mexican free-tailed bat	Extreme	7. 20	4. 30	7. 6	0. 65
Leaf-nosed bat	Great	4. 83		9. 5	0
Big brown bat	do	4. 50	4. 30	12. 8	1. 08
Pallid bat	do	2. 25		14. 3	. 66
Big-eared bat	do	1. 67		13. 0	1. 50
Big free-tailed bat	do			15. 2	1. 50
Small-footed myotis	Occasional	3. 40		14. 5	. 75
Western pipistrelle	do	<2. 00		14. 5	1. 49
Silver-haired bat	do	3. 17		15. 8	1. 50
Hoary bat	Infrequent	4. 70	5. 50	14. 1	1. 83
Red bat	do	4. 83	5. 80	16. 8	1. 18

[1] Bat species are arranged in order indicating greatest to least degree of expected association with the Mexican free-tailed bat.

[2] Intraspecific and interspecific gregariousness. Based on literature and observations of the author in the United States and Mexico.

[3] Numbers of 50 percent mouse lethal doses per 0.03 gram of bat tissue; given as exponent of 10. From data presented in tables 4 and 5.

[4] From table 4.

Table 7. **Responses of Carnivora to intramuscular inoculations [1] of tissue suspensions from bats infected with rabies**

Bat species origin of inoculum [2]	Inoculum range (MLD_{50}) [3]	Carnivora species							Course of disease		
		Dog	Cat	Fox	Coyote	Ringtail	Raccoon	Striped skunk	Days before death (mean)	Days ill (mean)	Signs of disease
Mexican free-tailed bat	832–4, 000	+	−	+	+	+	+	+	12. 7	<1. 0	Paralysis, furious ±
Leaf-nosed bat	795–15, 900	−	−	+	+	+	+	−	[4] 16. 5	5. 8	Furious, paralysis ±
Big brown bat	1, 500–5, 400	−	−	−	−	−	−	−			
Hoary bat	32–100, 000	−	−	−	−	−	−	−			
Red bat	600–6, 000	−	−	−	−	+	−	[5]+	22. 5	4. 0	Paralysis

[1] Data summarized from experiments described in references 4, 6, and 7.
[2] Bat species are arranged in an order indicating greatest to least degree of expected association with the Mexican free-tailed bat.
[3] 50 percent mouse lethal doses.
[4] Excludes a 114-day incubation period in a raccoon.
[5] Negative results obtained in inoculation of spotted skunks.

isolation from the original stock of the rabies virus and other rabies virus. Thus, the frequency of reintroduction of the stock virus or of other virus into a species should be inversely proportional to the degree in which virus differentiation is possible in that species.

Highest virus titers were listed, because they possibly have greatest significance, since degeneration of virus activity is known to occur in certain instances as death of the host approaches and after death. Unfortunately, few or no titrations were done in many instances. Whereas virus with the highest titers occurred in the brain rather than in salivary glands of the Mexican free-tailed bats, the reverse was true in hoary bats and red bats; these data are in agreement with the quantitative data discussed previously.

Periods of incubation and morbidity in mice and Carnivora increased as association of the bat species (origin of the virus) with the Mexican free-tailed bat and gregariousness of the individual species decreased.

Members of six of the seven Carnivora species inoculated with rabies virus of Mexican free-tailed bat origin died. Only four of the Carnivora species succumbed to infection with virus of leaf-nosed bat origin, and none died after inoculation of rabies virus from either big brown bats or hoary bats. Members of only two Carnivora species died with rabies following inoculation with virus of red bat origin; surprisingly, none of eight foxes developed the disease, although that species was observed to be particularly susceptible to rabies viruses isolated from a fox (*50*), a striped skunk (*51*), the Mexican free-tailed bat (*4*), and the leaf-nosed bat (*7*).

Virus Transmission from Bats

Evidently intraspecific transmission of rabies virus occurs between bats, but no information is available concerning interspecific transmission. It appears that parent-to-offspring transmission of virus occurs, but the route is obscure. Suckling Mexican free-tailed bats found in a roost under a bridge were infected with the virus as were others found in caves (*8, 9*). Yellow bat sucklings (*L. intermedius floridanus* [*D. floridanus*]) were reported positive to tests for rabies virus after the bats were collected from shelters in Spanish moss (*29*). Investigations indicated intraspecific transmission of the virus between red bats and between Mexican free-tailed bats may be possible by the bite route (*4, 6*), but the possibility of rabies transmission by aerosol or other routes between bats of the same or dissimilar species remains unclear (*9*).

Five cases of transmission of rabies virus from insectivorous bats to man have been reported in the United States (*52*). Three transmissions were by bite, and two were by a nonbite route, possibly by aerosol (*2, 9*). The silver-haired bat was responsible in one rabies death caused by a bite (*36*), and Mexican free-tailed bats were implicated in the deaths which resulted from nonbite transmission of virus.

Laboratory rodents were infected from bites of leaf-nosed bats and red bats which had been experimentally infected with rabies virus, but bites of similarly infected silver-haired bats, big brown bats, or hoary bats did not infect rodents (*6*, *7*). However, Bell achieved rabies transmission by permitting bats infected in nature (long-eared myotis, California myotis, silver-haired bat, and big brown bat) to bite suckling laboratory white mice (*47*).

No rabies developed in certain wild and domestic Carnivora species bitten by leaf-nosed bats or red bats experimentally infected with rabies virus. However, some Carnivora species were susceptible to infection from intramuscular inoculations of these viruses (*4, 6–8*). Carnivora failed to develop rabies from bites of silver-haired bats experimentally infected or from bites or intramuscular inoculations of virus from big brown bats or hoary bats. A partially paralyzed but furiously rabid pallid bat, found infected in New Mexico, failed to cause rabies deaths in a coyote and a fox experimentally bitten (on nose, tongue, labial mucosa, inguinal and axillary skin); at death, 5 days later, active rabies virus was recovered from the bat's brain, but its salivary glands were virus positive only by the FA test.

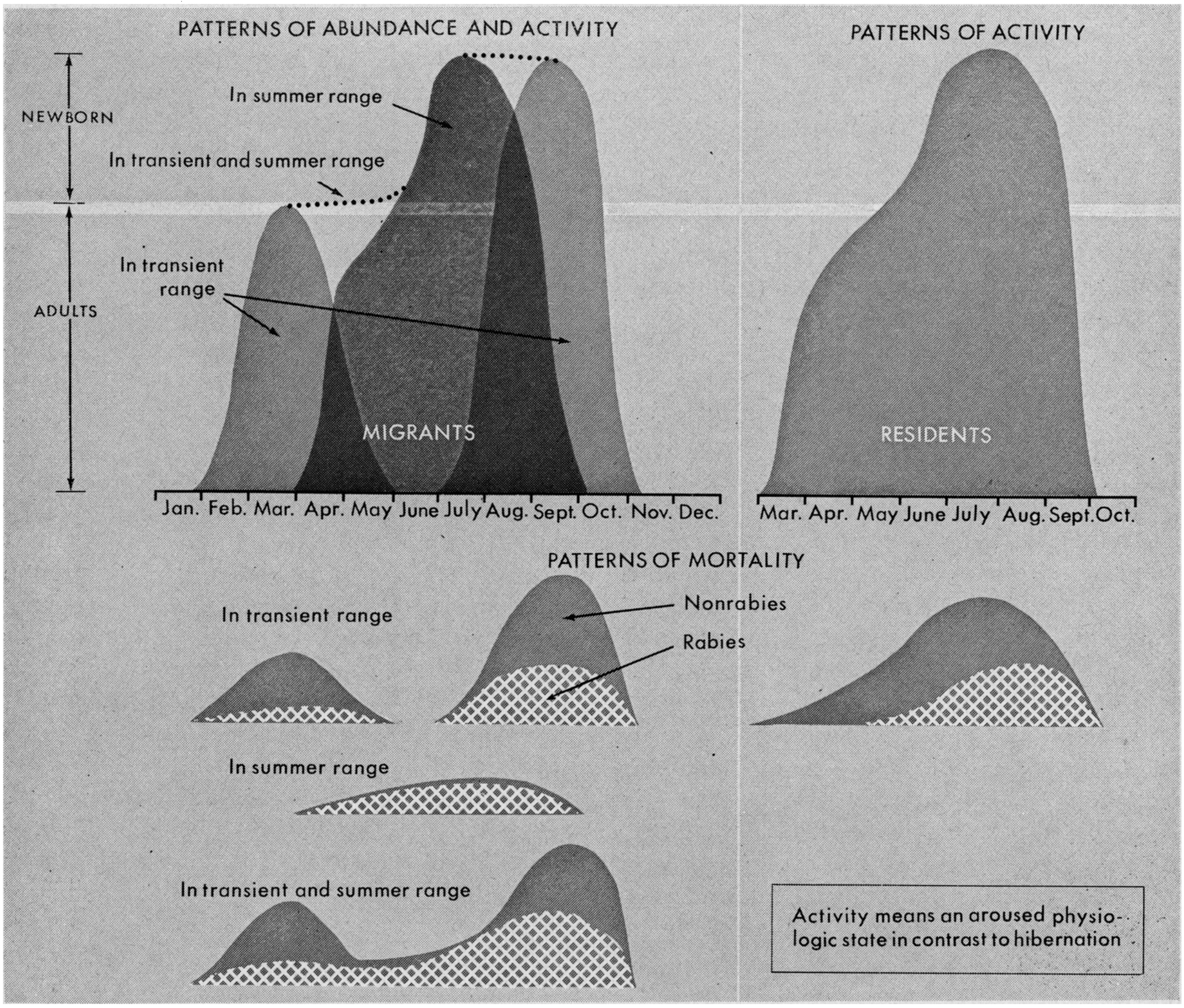
In some experiments, Carnivora did not develop rabies after bites of Mexican free-tailed bats (infected in nature or in the laboratory) or from eating rabies-suspect bats, but certain species of Carnivora were susceptible to infection by intramuscular inoculation of the virus (*4, 8*). In other experiments, Carnivora died of rabies after bites of experimentally infected Mexican free-tailed bats (*5*), and Carnivora, opossums, and hamsters died of rabies after exposure in caves to infection via aerols (*2, 9*). Foxes and coyotes were particularly susceptible to infection with virus of free-tailed bat origin. Species that failed to develop rabies after exposure by air, bite, or intramuscular inoculation to virus of free-tailed bat origin were susceptible to inoculation with coyote-passaged rabies virus from a coyote infected by a nonbite route (*3*).

Discussion

Data available from the western United States do not support popular belief that an increase in bat rabies cases has occurred since the disease was first detected in the West in 1954. More bats were submitted for rabies tests in successive years, but the percent of samples positive for rabies infection did not increase. It appears unlikely that actual numbers of bats downed by other causes would increase in direct proportion to numbers of bats downed by rabies infection unless a corresponding increase had occurred in the bat population, an improbable development, according to what is known about these populations. The explanation seems to be that increasingly greater numbers of sick or dead bats have been submitted to health departments as public awareness of bat rabies has grown. Although similar numbers of bats may have been observed earlier, they were not submitted for study. One seems justified in suspecting that bat rabies may have been present in the United States long before it was detected in Florida in 1953 and that rabies infections transmitted by bats may have been misdiagnosed. Indeed, a death, which occurred after a person was bitten by a bat in Texas in 1951 was first diagnosed as bulbar poliomyelitis (*53*). Similarly, in Trinidad, deaths from rabies following bites of infected vampire bats were misdiagnosed for several years as acute poliomyelitis (*54, 55*). Previous to detection of bat rabies in the United States, sick or dead bats, perhaps rabies infected, were submitted regularly to museums, where many were preserved as study skins or in liquid preservatives.

Rates of rabies infection in samples of clinically normal bats usually were less than 1 percent. Higher rates, when discovered, were in samples of bats collected in autumn. Evidence indicated that extensive geographic transport of rabies virus results from bat migrations, and the virus may overwinter in migratory bats, which remain active in winter, and in resident bats, which hibernate. The red bat and the hoary bat, which were collected in Iowa and eventually

Figure 5. Models of activity and mortality of bats



died with naturally acquired rabies infections, developed the disease when they normally should have been south of Texas (*32*, *56*, *57*). The portions of incubation periods observed in four captive Mexican free-tailed bats, collected in Texas, were long enough for the bats to be far south of the United States before developing the disease, and two of these bats might have completed the return flight to the United States before developing signs of rabies. The two big-eared bats infected with rabies, mentioned under "Pathogenesis of Infections in Bats," were collected after they had hibernated all winter and were about to awaken naturally. Presumably, they would have developed signs of the disease 2 to 3 months after natural awakening.

Many factors determine the mortality observed in bats. Some of the factors are numbers of bats present; degrees of bat activity; degrees of stress associated with migration, reproduction, weather, and other situations; accidents; predation; and diseases. These vary with species, sex, and age of bats and the place and time of the observation. The opportunity for observation is also variable. Excessive numbers of migratory bats appear to die during migration compared with the period of their summer habitat. A real difference probably exists, since bats must find refuge in unfamiliar, frequently undesirable, or hostile locations during migration. On the other hand, many bats which sicken and die in their summer habitat may not be observed as readily because their roosts are concealed.

Data on detected rabies infections in various States frequently are confusing, because bat species are not identified, data on nonrabies mortality are discarded, or parameters of bat populations are generally unknown. Data on bat rabies mortality and nonrabies mortality, given in this paper, have been clarified through a general understanding of bat ecology. It appears appropriate to summarize the epidemiologic patterns delineated in "models," to facilitate orientation and reference in this field. Accordingly, model graphs have been constructed (fig. 5), which reflect seasonal patterns of bat abundance and activity and rabies and nonrabies mortality. Models are presented for migratory bats in transient range, summer range, and both combined, and for resident, nonmigratory bats. Mortality depicted in the figure during summer is greater than one would expect to observe, because it would occur under conditions of optimum concealment in specific habitat.

Bat activity (or effective abundance) and bat rabies mortality increase as the calendar year lengthens (fig. 5). Increasing activity results in a greater effective population density with proportionately greater contact frequency and stress. Rabies cases increase with time as incubations terminate and greater bat activity permits development of increasing numbers of primary and secondary cases. Serum neutralizing antibodies for rabies may be present in some bats and transferred prenatally to young bats, which experience a loss of this protection by autumn (*8*), perhaps contributing further to the buildup of cases at that season.

A decrease and eventual cessation of detectable rabies virus in bat tissues may be due to autosterilization, perhaps associated with a rabies-inhibiting factor (*58*). Loss of rabies virus activity in salivary glands occurred before death in numerous instances, and a loss also occurred in brain tissue in another instance when the virus was still detectable (by FA test only) in salivary glands (*5*).

Man may be bitten more often by smaller species of bats because he handles the larger species with greater caution, or the smaller species may bite more readily. The five unprovoked attacks on man were by bats of smaller species. Of the five, the four identified as to species were members of the three smallest North American bat species: the western pipistrelle, the California myotis, and the small-footed myotis. The fifth bat, evidently a member of the genus *Myotis*, was not classified to species level. An indication of greater tendency to bite, coupled with known unprovoked attacks, may suggest a relatively high proportion of furious rabies in infected bats of the small species.

These species are known to have more in common than small size. They are permanent residents. They are solitary; usually only one or perhaps several live together except when young are born. They use narrow slots in stone or wood as shelter, which often precludes sharing the shelter with larger bat species. Pipistrelles are known to be pursued, captured, and eaten by hoary bats (*59*, *60*); cannibalism among bats is not uncommon in captivity, and smaller species may be attacked by larger bats in nature more frequently than reports indicate.

Because of its size, a small bat bitten by an infected bat should receive a wound of relatively maximum penetration and a greater dose of rabies virus per unit of body weight. Furious rabies is commonly seen in bats experimentally infected with rabies virus, but it appears unusual in nature. However, bats experimentally infected with virus are usually inoculated by the intracranial route; moreover, the doses they receive may differ from doses received in nature.

Furious rabies would favor virus transmission (and virus survival) in the small, solitary species, which apparently have fewer opportunities for the casual intraspecific biting frequently observed in gregarious bats.

A gradient in characteristics of rabies viruses in bats is suggested by data in tables 6 and 7, corresponding to known gradients in geographic and ecologic distributions, and gregariousness of host species. This gradient may reflect a similar route of virus exchange (past or continuing) between bat species, different rates of virus passage within each species, or different methods of virus transmission within each species.

The public health hazard of bat rabies is evident in relation to direct transmission from bats to man. Three persons were infected by bites of certain bat species, and evidently two persons were infected from another species of bat by the aerosol route. Knowledge of the indirect hazard which may exist by rabies virus transmission from bats to other species is incomplete. It appears possible that certain Carnivora or other animals may be infected by the airborne route in densely populated bat caves, but there are not many places where this may occur. However, partially paralyzed, rabies-virus infected bats that fall to earth at their roosts or while flying seem to present a generally distributed hazard to inquisitive animals and man.

Transmission of rabies virus from bats to Carnivora by bat bite occurred in only one of several experiments. Many species of bats have been shown to be capable of transmitting the rabies viruses they harbor to laboratory rodents by the bite route, but what this means concerning their ability to transmit the disease to man or Carnivora is not clear. However, in two instances bitten rodents died with rabies virus infections, but susceptible Carnivora species did not, indicating the limiting factor was the size of the dose transmitted in the bat bites. In instances in which all species failed to develop rabies after intramuscular inoculations of virus, it appears that the limiting factor may not have been dose size. Differences in results of transmission experiments, sometimes with conflicting results concerning virus from the same species of bat, serve to emphasize the need for additional experiments, permitting a better sampling of rabies virus isolates from each bat species.

Attempts to correlate the distributions of bat rabies and Carnivora rabies in time and space are plagued by difficulties. Although reliable data on population densities of bats or Carnivora are few, apparently both mammal groups are relatively abundant in similar habitat, particularly during warm months. Both abound where water, vegetation, and other forms of life are present in abundance.

Case reports are biased by space and time distributions because cases must be observed and reported by man, and the degrees of opportunity and effort vary. Generally, frequency of reporting is proportional to the density of the human population (thus the pet population also), and man usually resides in or near areas considered good for bats and native Carnivora. Man's outdoor excursions increase in frequency and extent during warm months, increasing chances of observing rabid animals at such times. Rabid Carnivora are more readily noticed and reported in rural areas than paralyzed bats, which are less conspicuous in the rough terrain. In addition, livestock owners are alert to the proved hazard of rabid Carnivora infecting domestic animals, and the incentive to report them is greater. Scatterday and co-workers (*61*) noted certain of these problems in Florida.

Bell (*47*) cited persuasive evidence that bats may not transmit rabies to Carnivora in Montana, since that State was nearly free of the disease in pets and livestock for many years despite the presence of the disease in bats. Fredrickson and Thomas (*62*) noted an interesting correlation between geographic distributions of rabid foxes and caves in Tennessee. In another study, rabies virus infection was found in one raccoon and two skunks (5.1 percent) of 59 native Carnivora (40 raccoons, 12 skunks, three foxes, and four opossums) trapped in Texas adjacent to caves occupied by great numbers of Mexican free-tailed bats (*9*). Only one of these three rabies-virus isolates produced incubation periods in mice as short as periods produced by virus of Mexican free-tailed bat origin; the other two isolates produced longer incubation periods, similar to the periods after inoculations of rabies virus from native Carnivora found in other areas in Texas. Thus, one animal, a raccoon, may have been infected from bats, but final proof could not be obtained.

Natural transmission of rabies virus to bats by bites of infected Carnivora appears possible as a rare event. However, the evidence at hand indicates that an independent rabies virus cycle exists in bats. Transmission of the virus from bats to Carnivora, should it occur in nature, would be tangential to that cycle, though a possible source of Carnivora rabies outbreaks. Paths of virus exchange between bat species and between bats and Carnivora should be delineated and their significance evaluated if we are to recognize links in the epidemiologic chain where appropriate and effective control can be applied.

Summary

Data on rabies observed in bats in California, Arizona, New Mexico, and Colorado for periods from 3 to 12 years were examined. Diagnoses of rabies were confirmed by the fluorescent antibody or serum-virus neutralization test.

Rates of rabies virus infection in clinically normal bats usually were no greater than 1 percent in resident bats but 2 to 3 percent in migratory bats. Highest rates were detected in autumn. Available evidence does not support the belief that bat rabies mortality has increased since rabies in bats was discovered in the United States. When mortality was examined with allowances for annual activity patterns of the hosts, a gradual increase in mortality was evident from spring to autumn. Considerable nonrabies mortality was observed, particularly in migratory bats.

Persons who encountered live bats infected with rabies experienced bites in a ratio of 14.2 bites per 100 live bats. Contacts between pets and bats occurred in a ratio of 29.8 pets per 100 infected bats. Bite rates were highest for bat species of smaller sizes, species making the few confirmed, unprovoked attacks.

Captive bats died of rabies infection after periods as long as 90 days, indicating that migratory bats would have carried the virus great distances, concurrently providing an overwintering mechanism in some instances. Nonmigrant bats, collected as they were about to awaken naturally from hibernation, died of rabies-virus infection several months later, illustrating another overwintering mechanism of the virus.

Rabies virus was present in the brains of all infected bats. Virus inactivation before death was observed in some tissues of bats infected in nature and in experiments. Bats frequently survived experimental exposures, some with no disease signs, some after recovering from rabies signs, and others with sequelae. Differences in bat rabies virus isolates were characterized by the responses of mice and Carnivora to infection.

In addition to the aerosol route of rabies virus transmission observed in bat caves, certain bats, under experimental conditions, transmitted infective doses of virus to Carnivora by biting them. Transmission of rabies virus to Carnivora species by bites of certain bat species could occur in nature, particularly when such animals investigate ill bats. Transmission of virus to Carnivora appears to be tangential to the cycle in bats but, if it occurs, it may prove to be significant.

REFERENCES

(*1*) Venters, H. D., Warren, R. H., Scatterday, J. E., and Hardy, A. V.: Rabies in bats in Florida. Amer J Public Health 44: 182–185, February 1954.

(*2*) Constantine, D. G.: Rabies transmission by nonbite route. Public Health Rep 77: 287–289, April 1962.

(*3*) Constantine, D. G.: Transmission experiments with bat rabies isolates: Responses of certain Carnivora to rabies virus isolated from animals infected by nonbite route. Amer J Vet Res 27: 13–15, January 1966.

(*4*) Constantine, D. G.: Transmission experiments with bat rabies isolates: Reaction of certain Carnivora, opossum, and bats to intramuscular inoculations of rabies virus isolated from free-tailed bats. Amer J Vet Res 27: 16–19, January 1966.

(*5*) Constantine, D. G.: Transmission experiments with bat rabies isolates: Bite transmission of rabies to foxes and coyote by free-tailed bats. Amer J Vet Res 27: 20–23, January 1966.

(*6*) Constantine, D. G., and Woodall, D. F.: Transmission experiments with bat rabies isolates: Reactions of certain Carnivora, opossums, rodents, and bats to rabies virus of red bat origin when exposed by bat bite or by intramuscular inoculation. Amer J Vet Res 27: 24–32, January 1966.

(*7*) Constantine, D. G., Solomon, G. C., and Woodall, D. F.: Transmission experiments with bat rabies isolates: Responses of certain Carnivora and rodents to rabies viruses from four species of bats. Amer J Vet Res. In press.

(*8*) Constantine, D. G., Tierkel, E. S., Kleckner, M. D., and Hawkins, D. M.: Rabies in New Mexico cavern bats. Public Health Rep. In press.

(*9*) Constantine, D. G.: Rabies transmission by air in bat caves. PHS Publication No. 1617. U.S. Government Printing Office, Washington, D.C. In press.

(*10*) State of California Department of Public Health: Rabies. California statistical report tables 1922–1960. Berkeley, 1965.

(*11*) State of California Department of Public Health: Rabies. California statistical report tables 1960–1964. Berkeley, 1965.

(*12*) Johnson, H. N.: Rabies. *In* Diagnostic procedures for viral and rickettsial diseases, edited by E.

H. Lennette and N. J. Schmidt. American Public Health Association, New York, 1964, pp. 356–380.

(13) Johnson, H. N.: The Rio Bravo virus: Virus identified with group B arthropod-borne viruses by hemagglutination inhibition and complement fixation tests. *In* Proceedings of the Ninth Pacific Science Congress, Bangkok, 1962, vol. 17, p. 39.

(14) Constantine, D. G., and Woodall, D. F.: Latent infection of Rio Bravo virus in salivary glands of bats. Public Health Rep 79: 1033–1039, December 1964.

(15) Bell, J. F., and Thomas, L. A.: A new virus, "MML", enzootic in bats (*Myotis lucifugus*) of Montana. Amer J Trop Med 13: 607–612, July 1964.

(16) Downs, W. G., et al.: Tacaribe virus, a new agent isolated from *Artibeus* bats and mosquitoes in Trinidad, West Indies. Amer J Trop Med 12: 640–646, July 1963.

(17) Sulkin, S. E.: The bat as a reservoir of viruses in nature. Progr Med Virol 4: 157–207 (1962).

(18) Boulger, L. R., and Porterfield, J. S.: Isolation of a virus from Nigerian fruit bats. Trans Roy Soc Trop Med Hyg 52: 421–424, September 1958.

(19) Lumsden, W. H. R., Williams, M. C., and Mason, P. J.: A virus from insectivorous bats in Uganda. Ann Trop Med Parasit 55: 389–397, December 1961.

(20) Bres, P., and Chambon, L.: Isolement a Dakar d'une souche d'arbovirus des glandes salivaries de chauve-souris. Ann Inst Pasteur (Paris) 104: 705–711, May 1963.

(21) Bres, P., et al.: Techniques pour l'etude de l'infestation naturelle des chauves-souris par les arbovirus. Interet epidemiologique au Senegal. Ann Inst Pasteur (Paris) 107: 34–43, July 1964.

(22) Williams, M. C., Simpson, D. I. H., and Shepherd, R. C.: Bats and arboviruses in East Africa. Nature (London) 203: 670, August 1964.

(23) Dean, W. D., Maddy, K. T., Cockrum, E. L., and Crecelius, H. G.: Rabies in insectivorous bats in Arizona. Arizona Med 17: 69–77, February 1960.

(24) Enright, J. B., Sadler, W. M., Moulton, J. E., and Constantine, D.: Isolation of rabies virus from an insectivorous bat (*Tadarida mexicana*), in California. Proc Soc Exp Biol Med 89: 94–96 (1955).

(25) Bell, J. F., Hadlow, W. J., and Jellison, W. L.: A survey of chiropteran rabies in Montana. Public Health Rep 72: 16–18, January 1957.

(26) Verts, B. J., and Barr, T. R. B.: An effort to identify rabies in bats from northwestern Illinois. Cornell Vet 51: 384–387, July 1961.

(27) Daniels, J. B., et al.: A search for encephalitis and rabies in bats of eastern Massachusetts. New Eng J Med 263: 516–520, September 1960.

(28) Girard, K. F., Hitchcock, H. B., Edsal, G., and MacCready, R. A.: Rabies in bats in New England. New Eng J Med 272: 75–80, January 1965.

(29) Schneider, N. J., et al.: Rabies in bats in Florida. Amer J Public Health 47: 983–989, August 1957.

(30) Tjalma, R. A., and Wentworth, B. B.: Bat rabies—Report of an isolation of rabies virus from native Ohio bats. J Amer Vet Med Assoc 130: 68–70, January 1957.

(31) Constantine, D. G.: Ecological observations on lasiurine bats in the north bay area of California. J Mammal 40: 13–15, February 1959.

(32) Constantine, D. G.: Ecological observations on lasiurine bats in Iowa. J Mammal 47: 34–41, March 1966.

(33) Constantine, D. G.: Spotted bat and big free-tailed bat in northern New Mexico. SW Naturalist 6: 92–97, September 1961.

(34) Constantine, D. G.: Experiments on the effect of ambient temperature on naturally-acquired rabies infections in Mexican free-tailed bats. Zoonos Res. In press.

(35) Findley, J. S., and Jones, C.: Seasonal distribution of the hoary bat. J Mammal 45: 461–470, August 1964.

(36) Humphrey, G. L., Kemp, G. E., and Wood, G.: A fatal case of rabies in a woman bitten by an insectivorous bat. Public Health Rep 75: 317–325, April 1960.

(37) Lennette, E. H., Soave, O. A., Nakamura, K., and Kellogg, G. H., Jr.: A fatal case of rabies following the bite of a rabid bat (*Lasionycteris noctivagans*). Isolation and identification of the virus from vector and victim. J Lab Clin Med 55: 89–93, January 1960.

(38) Bell, J. F.: Transmission of rabies to laboratory animals by bite of a naturally infected bat. Science 129: 1490–1491, May 1959.

(39) Quist, K. D., Eads, R. B., and Conklin, A: Studies on bat rabies in Texas. J Amer Vet Med Assoc 130: 66–68, January 1957.

(40) Sullivan, T. D., et al.: Recovery of rabies virus from colonial bats in Texas. Public Health Rep 69: 766–768, August 1954.

(41) Burns, K. F., and Farinacci, C. J.: Rabies in nonsanguivorous bats of Texas. J Infect Dis 97: 211–218, September–October 1955.

(42) Burns, K. F., Farinacci, C. J., and Murnane, T. G.: Rabies in insectivorous bats of Texas. J Amer Vet Med Assoc 128: 27–31, January 1956.

(43) Johnson, H. N.: Rabies virus. *In* Viral and rickettsial infections of man, edited by T. M. Rivers and F. L. Horsfall, Jr. Ed. 4. J. B. Lippincott Company, Philadelphia, 1965, pp. 814–840.

(44) Silva, R. A., Rivello, G. V., and Nilsson, M. R.: Isolamento de virus rabico de morcego nao hematofago de especie *Phyllostomus hastatus hastatus* (Pallas). Arq Inst Biol Animal 4: 115–120 (1961).

(45) Tellez Giron, A.: El vampiro portador de virus del derriengue. Revista Soc Mexicana Historia Natural 5: 35–42, June 1944.

(46) Johnson, H. N.: Derriengue: vampire bat rabies in Mexico. Amer J Hyg 47: 189–204, March 1948.

(47) Bell, J. F., Moore, G. J., Raymond, G. H., and Tibbs, C. E.: Characteristics of rabies in bats in Montana. Amer J Public Health 52: 1293–1301, August 1962.

(48) Avery, R. J., and Tailyour, J. M.: The isolation of the rabies virus from insectivorous bats in British Columbia. Canad J Comp Med 24: 143–146, May 1960.

(49) Scatterday, J. E., and Galton, M. M.: Bat rabies in Florida. Vet Med 49: 133–135, April 1954.

(50) Sikes, R. K.: Pathogenesis of rabies in wildlife. 1. Comparative effect of varying doses of rabies virus inoculated into foxes and skunks. Amer J Vet Res 23: 1041–1047, September 1962.

(51) Parker, R. L., and Wilsnack, R. E.: Pathogenesis of skunk rabies virus: Quantitation in skunks and foxes. Amer J Vet Res 27: 33–38, January 1966.

(52) Tierkel, E. S.: Rabies. *In* Diseases transmitted from animals to man, edited by T. G. Hull. Ed. 5. Charles C Thomas, Springfield, Ill., 1963, pp. 293–349.

(53) Sulkin, S. E., and Greve, M. J.: Human rabies caused by bat bite. Texas State J Med 50: 620–621, August 1954.

(54) Hurst, E. W., and Pawan, J. L.: An outbreak of rabies in Trinidad. Lancet 221: 622–628, Sept. 19, 1931.

(55) Pawan, J. L.: The transmission of paralytic rabies in Trinidad by the vampire bat (*Desmodus rotundus murinus* Wagner, 1840). Ann Trop Med Parasit 30: 101–131, April 1936.

(56) McClure, H. E.: Summer activities of bats (genus *Lasiurus*) in Iowa. J Mammal 23: 430–434, November 1942.

(57) Wiseman, J. S., Davis, B. L., and Grimes, J. E.: Rabies infection in the red bat, *Lasiurus borealis borealis* (Muller), in Texas. J Mammal 43: 279–280, May 1962.

(58) Wilsnack, R. E., and Parker, R. L.: Pathogenesis of skunk rabies virus: rabies inhibiting substance as related to rabies diagnosis. Amer J Vet Res 27: 39–43, January 1966.

(59) Bishop, S. C.: Curious behavior of a hoary bat. J Mammal 28: 293–294, August 1947.

(60) Orr, R. T.: Unusual behavior and occurrence of a hoary bat. J Mammal 31: 456–457, November 1950.

(61) Scatterday, J. E., Schneider, N. J., Jennings, W. L., and Lewis, A. L.: Sporadic animal rabies in Florida. Public Health Rep 75: 945–953, October 1960.

(62) Fredrickson, L. E., and Thomas, L.: Relationship of fox rabies to caves. Public Health Rep 80: 495–500, June 1965.

Education Notes

World Health Organization Fellowships. In 1968 the World Health Organization will make a limited number of short-term fellowships available for "improvement and expansion of health services" in the United States.

The awards, generally limited to 2–4-month periods, will cover per diem expenses and transportation. They will not be granted for conducting research projects or attending international meetings.

Applicants must be engaged in full-time public health or educational work in the United States, and their employers will be expected to continue their salaries during the fellowship term. Officers and employees of the U.S. Government are not eligible.

Deadline for receipt of applications is January 1, 1968, but fellowships probably will not start before May 1, 1968. Further information and application forms may be obtained from William S. Wilson, Public Health Service, Washington, D.C. 20201.

Principles of Chemical Epidemiology. A training course in the principles of chemical epidemiology is being sponsored by the Pesticides Program of the Public Health Service. It has been scheduled for November 28–30, 1967, at the National Communicable Disease Center.

The course is designed for epidemiologists, members of epidemiologic teams in State and local health departments, and employees of private or public agencies concerned with investigation of chemical poisonings.

Presentations will include lectures and demonstrations on aspects of pesticides, toxicology, chemical epidemiology, pesticide chemistry, and laboratory tests used to diagnose chemical poisonings.

Additional information may be obtained from the Chief, State Services, Pesticides Program, National Communicable Disease Center, Public Health Service, Atlanta, Ga. 30333.