Prepared by the USGS National Wildlife Health Center

Bat Rabies and Other Lyssavirus Infections

Circular 1329

U.S. Department of the Interior
U.S. Geological Survey

Front cover photo (D.G. Constantine)

A Townsend's big-eared bat.

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By Denny G. Constantine

Edited by David S. Blehert

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A pallid bat in flight. (D.G. Constantine)

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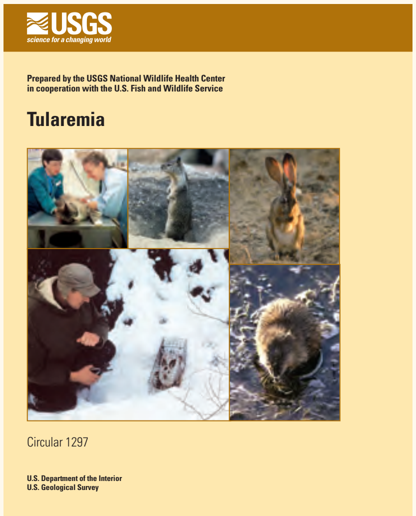

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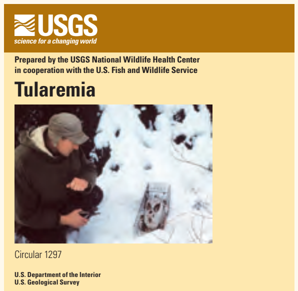

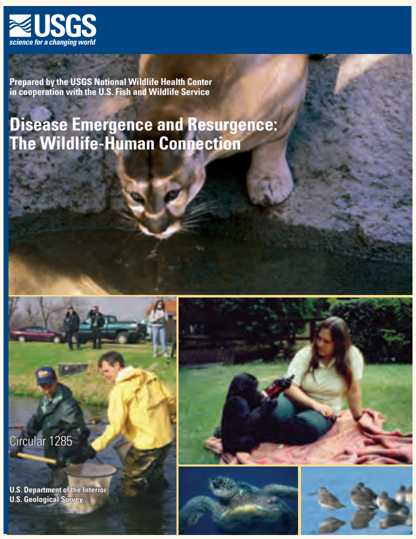

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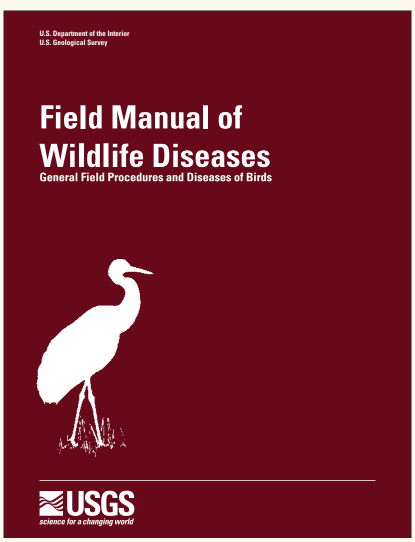

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Foreword

In many ways, bats are the nocturnal equivalent of birds (Kunz, 1982). Like birds, they consume large numbers of insects that cause harm to agriculture and to humans; researchers estimate that the value of bat control of cotton crop pests in eight counties in south-central Texas ranges from $121,000 to $1,725,000 per year (Cleveland and others, 2006). Bats also play an important role as pollinators and in spreading plant seeds by eating the fruits of some plants. The estimated 1,100 species of bats worldwide comprise about 20 percent of all mammal species (Tudge, 2000), are second only to rodents in number of species, and are likely the most numerous in total individuals of any type of mammal (Kunz 1982). Despite their important ecological roles and benefits to humans, bats are among the most maligned and mysterious animal group in existence, largely due to folklore and unfamiliarity with the true nature of these primarily nonhematophagous, or nonblood feeding, species (King, 1993).

The notoriety associated with rabies in vampire bats of the tropical and subtropical regions of the New World is unfortunately transposed by many to also reflect the demeanor and consequences of the presence of other types of bats. Clearly, vampire bat rabies was a prominent challenge for early Spanish colonists and their domestic animals during their settlement within Latin America (Baer, 1975a; Lopez and others, 1992). Because of vampire bat rabies, the presence of bats in urban environments of the Northern Hemisphere commonly elicits fear among many adults, but wonderment among the young and the young-at-heart. The former tend to associate the presence of bats with rabies, while the latter see only the uniqueness of these highly specialized flying mammals and often place themselves at risk by attempting to capture and handle these animals for closer examination.

Rabies in a nonhematophagous North American bat was not documented until 1953, when a yellow bat (*Dasypterus floridanus*, now *Lasiurus intermedius*, the Northern yellow bat) was examined following its aggressive biting of a 7-year-old boy in Florida. Fortunately, despite no previous documentation of rabies in insectivorous bats in the United States, the child received prompt postexposure prophylactic treatment for rabies and did not become clinically ill (Venters and others, 1954, Scatterday, 1954). Subsequent investigations resulted in retrospective diagnoses of bat rabies in the USA in 1951 and, possibly, even 30 years earlier, suggesting the presence of rabies in **insectivorous** bats long before its recognition (Baer, 1975b). During recent decades, an average of 700 to 800 cases of rabid insectivorous bats has been diagnosed annually in the USA (Rupprecht and others, 1995). During 2006, 1,692 cases of rabies were reported in bats, a 14.5 percent increase over 2005 and 24.4 percent of the total animal rabies cases. Only raccoons accounted for a greater number of rabies cases in the USA during 2006 (Blanton and others, 2007).

Although the annual number of human rabies deaths in the USA remains very small, most of those deaths are attributed to unrecognized exposures to rabies associated with bats, primarily the silver-haired bat and the tricolored bat, two infrequently encountered bat species. The ecological relationships driving such outcomes extend beyond evolutionary increases in viral infectivity reported for these bat species (Messenger and others, 2003). Equally, if not more important, are factors that result in human contact with these species. Human-induced landscape changes influence the distribution and abundance of animal populations, and these types of changes have had a major role in the ascension of wildlife rabies

(Rupprecht and others, 1995) and likely will continue to do so. Bat-associated human disease emergence during recent years includes Nipah, Marburg, "Melaka," and Hendra viruses, and human Nipah virus infections clearly result from landscape changes that cause the bats to relocate their roosts to sites where interspecies disease transmission is facilitated (Daniels and others, 2007). That outcome emphasizes the importance of understanding bat ecology as a component of disease ecology.

Knowledge of bat ecology is especially important when humans and bats share environments. This information is needed to properly educate people about bats and for the application of pre-emptive actions, including education, for minimizing disease risks that may be present. Simple, inexpensive means for bat exclusion noted in the text can be installed to permit bats to depart from but prevent re-entry into buildings. This text also stresses the importance of house cats in the transmission of bat rabies, a situation that can largely be controlled by preemptive actions identified by the author and that many readers may apply to their daily lives with their pet cats.

Of special importance is the potential for contact between children and bats. Young people are often at higher risk for exposure to rabid bats because their uninhibited curiosity may result in their handling of moribund and injured bats, including those that may have been captured by the family cat. This writer had several personal experiences evaluating bats that were picked up by students, brought to grade school biology classes, and that proved to be rabid. Fortunately, no human rabies cases resulted from those events.

Education about bats provides valuable balance so that disease risks are not overstated, fostering fear of these species, or understated to the extent that people are placed at undue risk. Personal experiences have indicated that private sector presentations by those interested in bat conservation often understate disease considerations and demonstrate risky behaviors, such as handling bats without protective gloves, in efforts to overcome negative perspectives of bats advanced by others. These same types of indiscretions also appear in various publications (King, 1993).

The best defense against potential disease risks posed by bats, or any animal species, is a sound understanding of disease ecology and the wise application of that knowledge. Through this publication, Dr. Constantine strives to provide the reader with these attributes by sharing over a half-century of personal experiences and scientific investigations of bat rabies ecology. During his career, Dr. Constantine has significantly contributed to the scientific knowledge of this complex disease and challenged existing dogma in ways that have enhanced our current understanding of rabies transmission (see literature citations associated with the text). This unique and highly informative presentation incorporates anecdotes as well as hard science to provide both nonscientists and specialists with numerous points to ponder and a better understanding of bats as part of our biological world. The presentation is enhanced by the many illustrations that portray diversity among bat species, some of their adaptive features, and other aspects of bat biology. Bats have successfully colonized most regions of earth except for Antarctica and some other treeless northern areas of extreme cold (Kunz, 1982). These species need to be conserved for their ecological importance and for the benefits that they provide humans, rather than feared because of disease.

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This publication is due in large part to the help and cooperation provided the author by a great variety of workers during a lifetime of his investigations. Those individuals worked in fields such as public health, wildlife health, wildlife ecology and conservation, animal control, and also included landowners and land managers. Space does not allow detailing their individual contributions or listing all of them. Instead, I thank the multitude of those who have assisted my efforts and note those field companions who have made relevant contributions recalled during the development of this report. I have greatly enjoyed probing the secrets of nature with all of these individuals, some of whom are listed below by geographic area of shared exploration.

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Worldwide: Kenneth G. Constantine

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Contents

Topic Highlight Boxes

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Words in **bold** type in the text, the topic highlight boxes, and the tables are defined in the Glossary.

"What shall I do? What can I do? How can I escape from this dreadful thing of night and gloom and fear?"

(Stoker, 1897)

"He who shall eat the tongue or the heart of a bat shall flee from water and die."

(Rhazes, 10th century Persian physician, quoted by Aldrovandi, 1599)

Top: A big brown bat drinking on the wing is reflected in the water below. (D.G. Constantine)

Bat Rabies and Other Lyssavirus Infections

By Denny G. Constantine

Synonyms

Rabia en murciélagos (Spanish)
Raiva em morcegos (Portuguese)
Rage de chauves-souris (French)
Tollwut bei fledermäusen (German)

Overview

Rabies constitutes a nearly global viral disease of **mammals** that affects the central nervous system, is usually transmitted by bite, and typically results in the death of the **host**. The causative agent is a member of the **lyssavirus** group (Niezgoda and others, 2002). Each Lyssavirus **species** is divisible into **strains** called **variants**, each of which usually is found only in an individual **reservoir host** species of **carnivore** (Order Carnivora) or **bat** (Order Chiroptera), within which the **virus** multiplies (Table 1; Rupprecht and others, 2001). Humans and other species are infected through contact with a host animal. Bats are the focus for this synopsis (Box 1), and they are known to be infected throughout the **Americas** and in Europe, Asia, Africa, and Australia (Niezgoda and others, 2002). Both suborders of bats, the **Megachiroptera** or large fruit-eating bats of the Old World tropics, and the **Microchiroptera**, consisting of all other bats distributed globally to the limits of tree growth, are known to become infected with variants of lyssavirus. Bat species known to be rabies infected in the USA and the Americas are listed in Appendixes A and B, respectively.

Background

The origin of rabies, as of many other infectious diseases, is a matter of speculation. It has been postulated that rabies viruses may have originated from an insect virus that infected insect-eating bats some 7,000 to 12,000 years ago (Badrane and Tordo, 2001). Three such insect viruses, proposed for inclusion in the Lyssavirus **genus**, are known today. Moreover, data and calculations have been presented to support the view that after rabies viruses evolved in bats between 900 to 1,500 years ago, the infection subsequently spilled over into carnivorous mammals (Badrane and Tordo, 2001). Bats and carnivores are essentially the only natural or persistent reservoir hosts of rabies known today, and individuals of other mammal species usually die without spreading the infection.

North American bats north of Mexico, nearly all of them insectivorous, were ignored as potential rabies hosts until 1953 when the father of a bitten child, aware of the infection spread by vampire bats, insisted that the biting bat be tested. After the bat was determined to be rabid (Venters and others, 1954), surveys were conducted until the virus was found throughout the continent in all bat species that were extensively tested. Whereas only 0.1 percent of seemingly healthy bats were infected, 10 percent of bats that were rabies-suspect, because they were found ill or were dead, were positive for rabies infection (Constantine, 1988a).

Findings in North America soon stimulated surveys throughout the world. These surveys focused on sampling colonies of healthy bats, and they generally yielded negative results, such as those from North America. However, the testing of **symptomatic** bats eventually produced rabies viruses that differ from typical carnivore rabies isolates (Hentschke and Hellman, 1975; Mohr, 1957; Pitzschke, 1965). Interest in bat rabies has varied with time. For example, European bat rabies was identified in the laboratory only 14 times over 30 years. Then, in 1985, three European human rabies deaths following bat bites were reported (Lumio and others, 1986; Selimov and others, 1986), causing such increased effort that by the end of 1989, 4,705 European bats had been tested, 379 (8 percent) of which were found to be infected (Kappeler, 1989). Additional cases in bats and other mammals were discovered in Africa and Asia. In Australia, where rabies was believed to be absent, rabies infection was reported in adequately sampled bat species ranging from small insect-eaters to large fruit-eating bats known as flying foxes.

Causative Agent

Classical rabies has been known for centuries and it is caused by the most widespread of seven similar virus species (also called **genotypes**, as each species is defined by phylogenetic analysis of viral genes) within the genus Lyssavirus (McColl and others, 2000). Four additional **putative** Lyssavirus species were discovered recently and their **taxonomic** positions are under study (Kuzmin and others, 2005) (Fig. 1). Discoveries of additional lyssaviruses are likely to follow. Whereas classical rabies is well known, other lyssavirus species were not identified prior to 1956; thus, far less is known about them. For practical purposes, all lyssavirus species potentially produce rabies-like infections, so all are included in this publication. Lyssavirus is an appropriate name for these viruses as "lyssa" means rage, fury, or canine madness in Greek.

Table 1. Lyssavirus infections in mammals: agents, hosts, identification, and effectiveness of antirabies prophylaxis measures for humans.

Lyssavirus type		Known hosts		Diagnostic capabilities [3]	Effectiveness of antirabies prophylaxis for humans [4]
Name	Genotype	Reservoirs [1]	Victims		
Rabies	1	Carnivores, American bats	Humans, other mammals	Most government laboratories	Satisfactory.
Australian bat	7	Australian bats	Humans	Most government laboratories	Satisfactory.
European bat-2	6	European bats	Humans	Major regional	Reduced.
Irkut bat	Unclassified	Asian bats	Ferrets [2]	Major regional	Reduced.
Aravan bat	Unclassified	Asian bats	Hamsters [2]	Major regional	Reduced.
Khujand bat	Unclassified	Asian bats	Ferrets [2]	Major regional	Reduced.
European bat-1	5	European bats	Humans, cats, stone marten, sheep	Major regional	Poor.
Duvenhage bat	4	African bats	Humans	Major regional	Poor.
Mokola	2	African shrews and insectivorous rodents	Humans, dogs, cats	Major regional	None.
Lagos bat	3	African bats	Dogs, cats, mongooses	Major regional	None.
West Caucasian bat	Unclassified	Eastern European bats	Hamsters [2]	Major regional	None.

[1] A species that maintains the virus in nature. Reservoir species may also succumb to infection.

[2] Experimental infections.

[3] Disease diagnostic laboratories capable of isolating the virus and identifying the genotype.

[4] Degree of protection estimates based primarily on laboratory animal responses (Hanlon and others, 2005).

Vampires, Werewolves, and Settlement of the Americas Box 1

Bat-borne rabies, perhaps especially involving common vampire bats, may have inspired or influenced early tales of human vampires in Europe. The patterns of **serial transmission** by bite and the dreadful transformation of victims are strikingly similar. Correspondingly, rabies may have contributed to tales of werewolves and the transformation of their worldwide counterparts into various carnivorous mammals, perhaps influenced by cases of "barking" human rabies victims or of attacks by some infected human victims on other people.

Common vampire bat in a Venezuelan cave. (D.G. Constantine)

Vampire bats also were likely causes of rabies prior to the arrival of European explorers in the Americas, and the rabies-like deaths of explorers in tropical America caused by "venomous bites" of vampire bats were reported in the 16th century. At that time, native peoples attempted to prevent rabies infections by cleansing the sites of vampire bat bites and cauterizing the wounds with wood embers (d'Anghiera, 1555; De Oviedo y Valdes, 1526). Subsequent outbreaks of rabies in humans and their domestic animals plagued Latin America and prevented the development of extensive areas, problems that continue today. The infection eventually was found in various other tropical American bat species that specialize in diets consisting of fruit, pollen, nectar, insects, fish, or other vertebrates.

Prudence suggests that all lyssaviruses should be regarded as dangerous as classical rabies and, thus, likely to be lethal for humans and other mammals. The hazards can be even greater because not all of these viruses are readily identifiable by standard rabies diagnostic methods (Table 1). Furthermore, except for Australian bat lyssavirus, other lyssavirus infections are not dependably preventable by available rabies **vaccines** and rabies **hyperimmune sera**. For example, no **biologics** are available to prevent infection from the Lagos bat, Mokola, or West Caucasian bat viruses, and current rabies biologics have variably reduced effectiveness against the other currently known lyssaviruses (Hanlon and others, 2005).

Based on knowledge of rabies and most other lyssaviral species, each lyssaviral species may prove to be divisible into variants. Each variant typically is found in a single species of reservoir host, and it apparently develops after its precursor is transmitted to a new host species. For example, a different bat lyssaviruss may evolve after it is transmitted from one bat species to another bat species, within which it subsequently reproduces in isolation, becomes differentiated from the original lyssavirus, and as time progresses, it becomes increasingly efficient in establishing itself in the second bat species. After a variant is transmitted from its reservoir host to an atypical or aberrant host species, a dead-end infection usually results because the maladapted atypical host quickly dies before the virus can be transmitted further. Identification of variants that infect atypical hosts, such as humans, usually points to a particular natural reservoir host species, such as a species of carnivore or bat, as the source for the human infection.

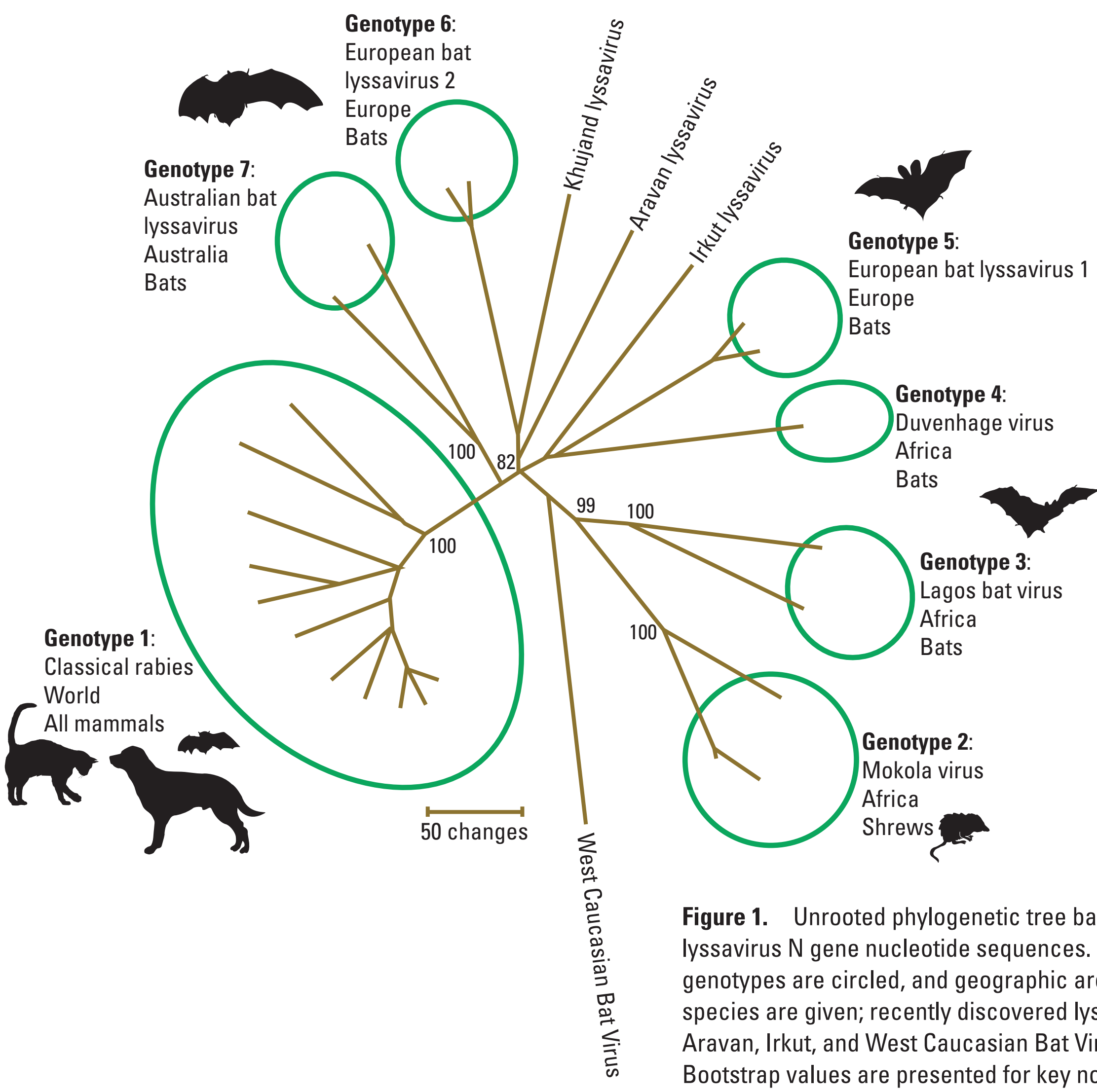


Figure 1. Unrooted phylogenetic tree based on complete lyssavirus N gene nucleotide sequences. Previously recognized genotypes are circled, and geographic area and primary host species are given; recently discovered lyssaviruses (Khujand, Aravan, Irkut, and West Caucasian Bat Virus) are not circled. Bootstrap values are presented for key nodes, and branch lengths are drawn to scale (Modified from Kuzmin and others, 2005; see also Kissi and others, 1995).

Geographic Distribution

Although bat lyssavirus infections have a broad geographic distribution (Figs. 2 and 3), our knowledge of lyssavirus distribution is incomplete for various reasons, including underreporting (Table 2). In some instances, reporting is inhibited by apprehension over the potentially suppressive effects on development or tourism. At best, reporting requires the presence of people to detect infected bats. For example, many cases in the USA are reported from cities, but unpopulated or sparsely populated areas often are devoid of reports. Nevertheless, lyssavirus infections have received considerable attention in the Americas and they are now known wherever bats are found. Eventually, lyssavirus infections may be found globally except for treeless areas and some isolated islands.

Patterns and Trends

Changes in human perception and increased research efforts have improved understanding of bat lyssavirus infections in bats, humans, and other mammals. Although vampire bat-borne rabies infected humans prior to European explorations in tropical America, the viral cause was not discovered until over 400 years later (Carini, 1911). Knowledge of the existence of vampire bat rabies stimulated research to enhance understanding of the extent and the gravity of infection and led to the development of methods for combating it. However, resource allocations for these efforts have been inconsistent and have fluctuated greatly. Consequently, the history of bat lyssavirus infections in general and their suppressive effects on geographic and economic development in the Americas are incompletely known. By 1969, the Food and Agricultural Organization of the United Nations concluded that cattle deaths and indirect losses caused by vampire bats cost Latin America over one-third of a billion dollars annually (Steele, 1969). Since then, relief has been provided through development of vampire bat control techniques and rabies vaccines. These advances have largely been supported and coordinated by the Pan American Health Organization (Belotto, 2005).

The 1953 discovery in the USA of bat rabies transmitted by bats other than the vampire bat (Appendix A) stimulated a major research effort that resulted in the disclosure of increasing numbers of cases (Fig. 4). These findings supported the popular conclusion that bat rabies was a new and growing problem. However, case increases proved to be proportional to investigative effort, with growing numbers of bats tested as time progressed (Fig. 5) (Constantine, 1967a). News coverage is another factor leading to local increases in the submission of bats to be tested and to corresponding increases in reported cases. In addition, technological advances have increased the application of rabies virus variant identification techniques and are yielding greater numbers of human rabies cases attributed to bats. During 2006, 1,692 cases of rabies in bats were reported in the USA.

Table 2. General geographic area of rabies-related lyssavirus infections reported in bats.

[Unknown indicates that the lyssavirus species was known only to be rabies-related]

Lyssavirus species	Number of bat species reported infected					
	Africa	Australia	Asia	Europe	Indian subcontinent	Middle East
Aravan			1			
Australian		5				
Duvenhage	1					
European-1				9		
European-2				7		
Irkut			1			
Khujand			1			
Lagos	4					1
West Caucasion				1		
Unknown	1		3	7	2	1
Total:	**6**	**5**	**6**	**24**	**2**	**2**

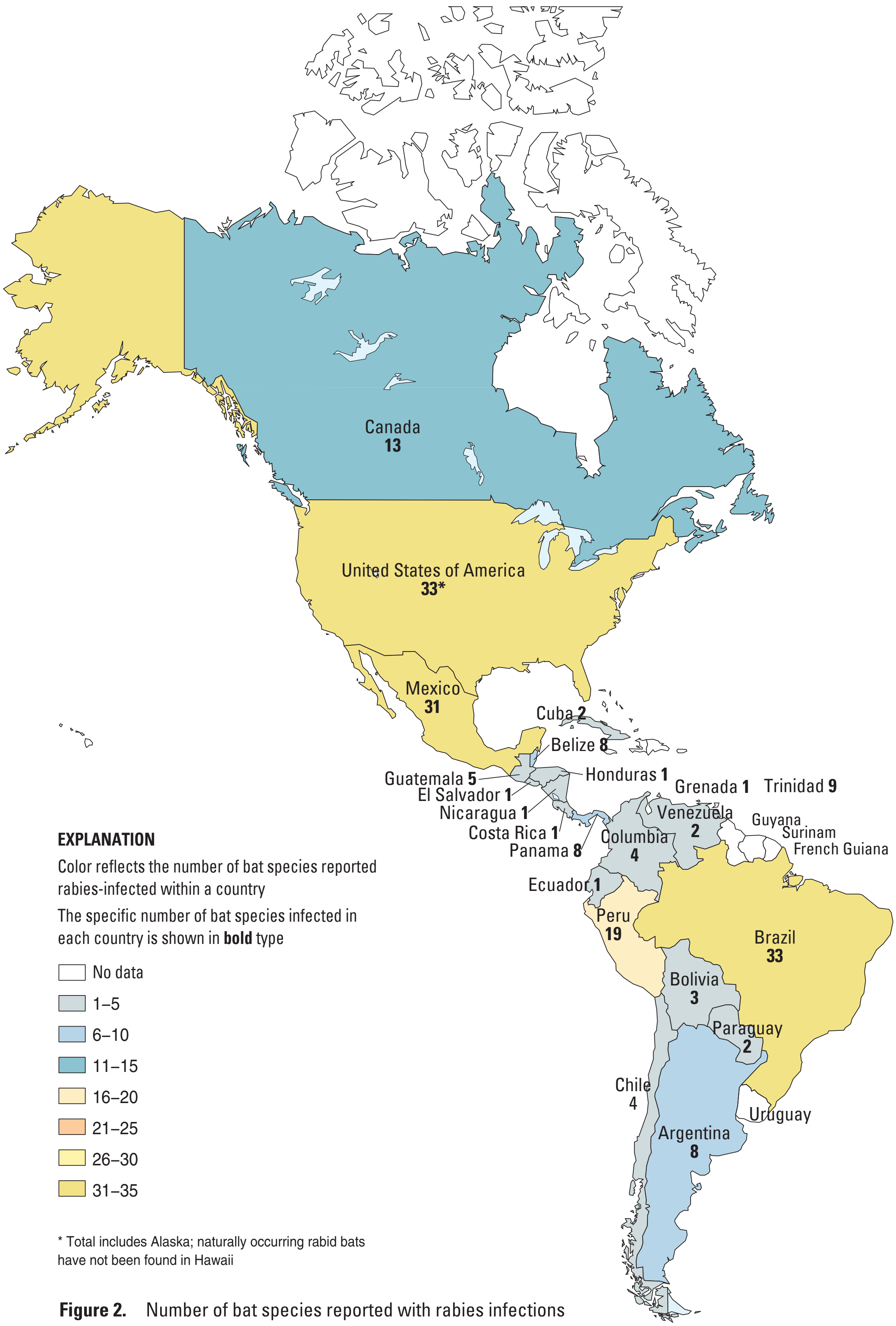


Figure 2. Number of bat species reported with rabies infections within the Americas (D.G. Constantine, unpub. data).

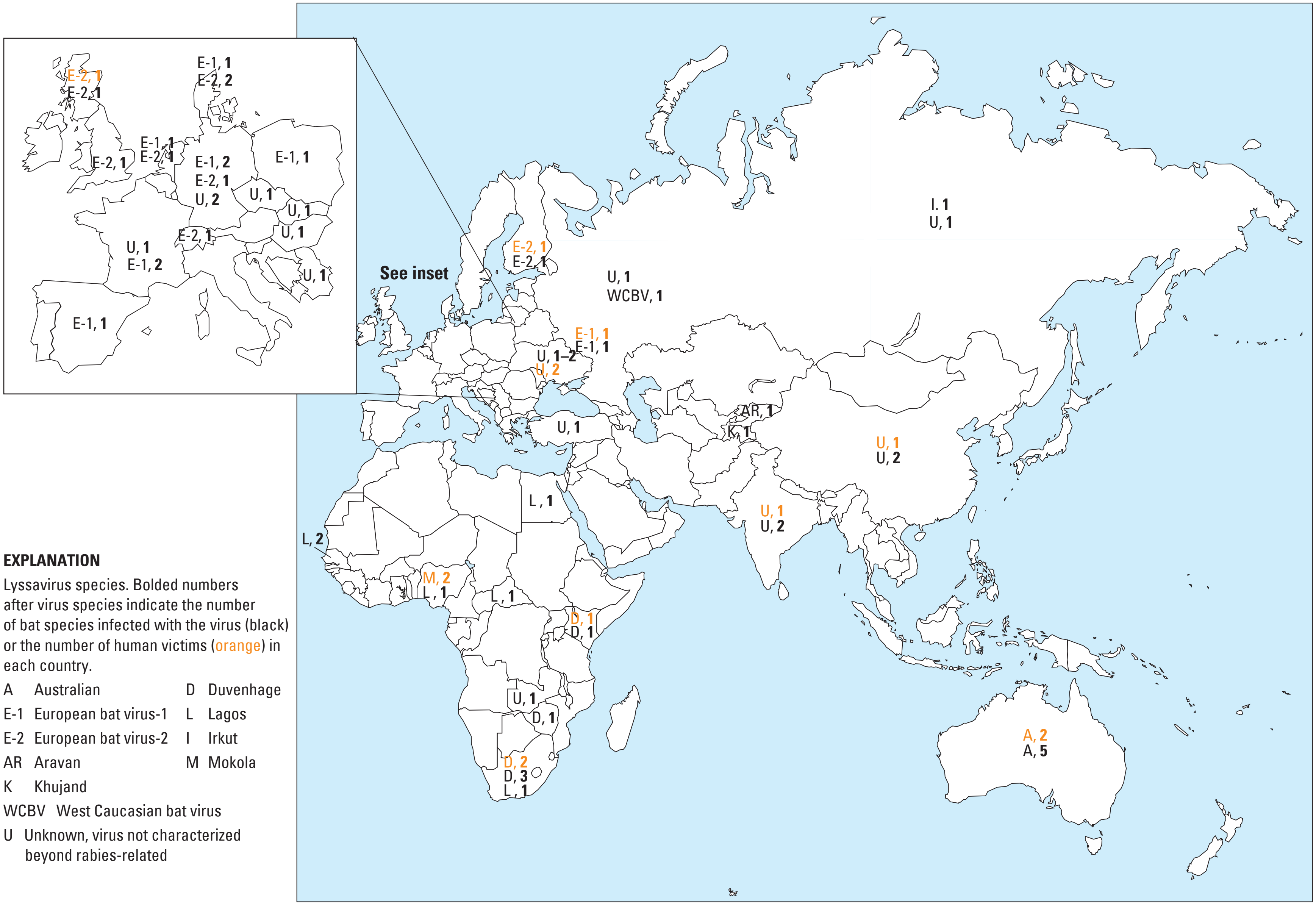


Figure 3. Old World distribution of lyssavirus infections (excluding rabies virus) reported in bat species (black) and humans (red) in Africa (Boulger and Porterfield, 1958; Crick and others; 1982; Foggin, 1988; Familusi and others, 1972; Foggin, 1988; Markotter and others, 2006a; Meredith and others, 1971; Paweska and others, 2006; Sureau and others, 1980; van Thiel and others, 2008), Asia (Arai and others, 2003; Kuzmin and others, 2003; Tang and others, 2005), Australia (Allworth and others, 1996; McColl and others, 2002; Warrilow and others, 2003), Europe (Amengaul and others, 1997; Botvinkin and others, 2003; Bruyère and Janot, 2000; Bruyère-Masson and others, 2001; Fooks and others, 2002; Hentschke and Hellman, 1975; Johnson and others, 2006; Kappeler, 1989; Kerekes, 1999; King and Crick, 1988; Khozinski and others, 1990; Kuzmin and others, 2005; Lumio and others, 1986; Matouch, 1999; Nikolíc and Jelesíc, 1956; Pérez-Jordá and others, 1995; Serro-Cobo and others, 2002; Tunçman, 1958; Selimov and others, 1991; Van der Poel and others, 2003; WHO Collaborating Centre for Rabies Surveillance and Research, 1999), the Indian subcontinent (Pal and others, 1980; Veeraraghavan, 1955), and the Middle East (Picard-Meyer and others, 2004).

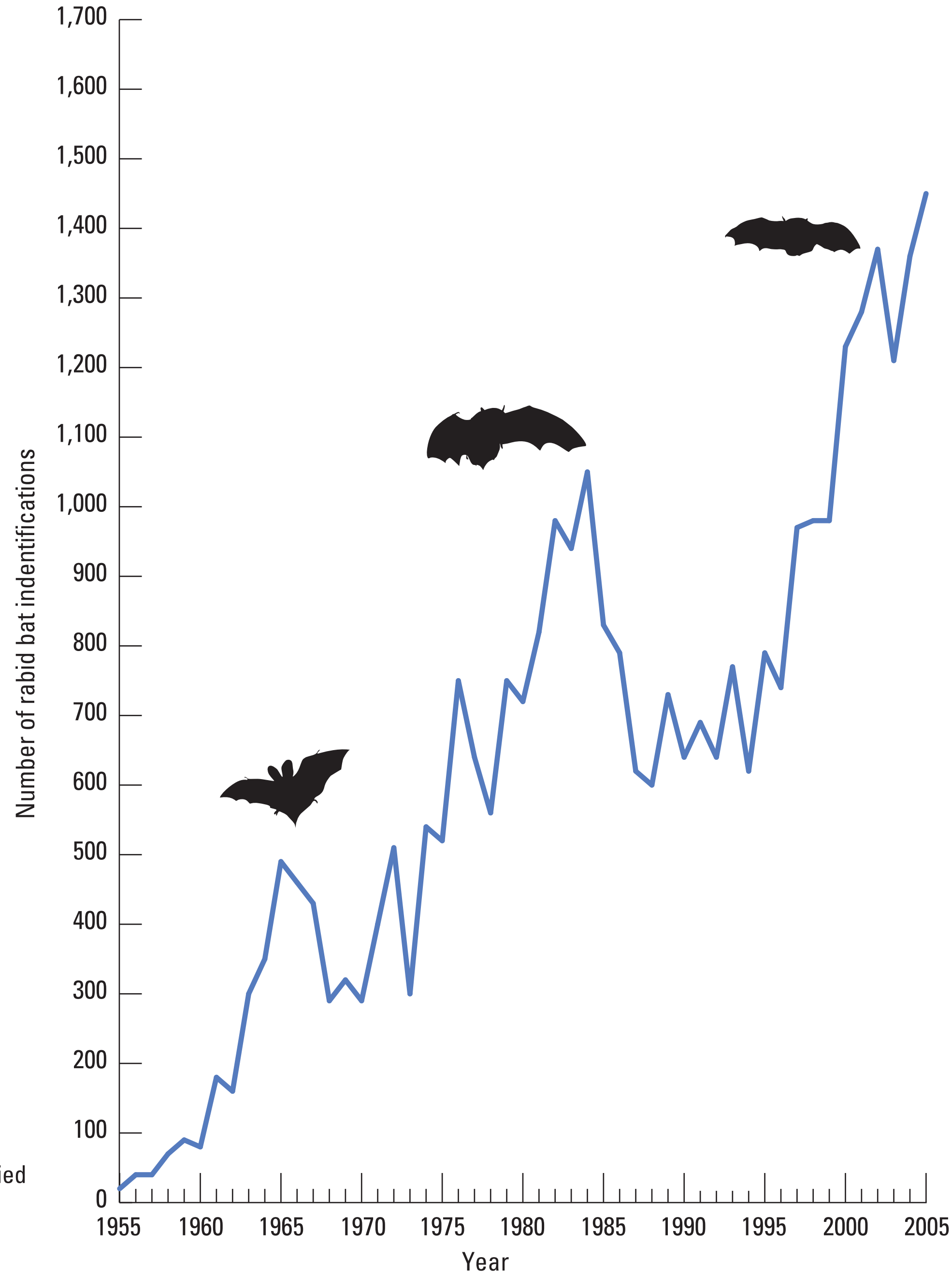


Figure 4. Number of rabid bats identified in the United States from 1955 to 2006. Compiled from U.S. Centers for Disease Control and Prevention data.

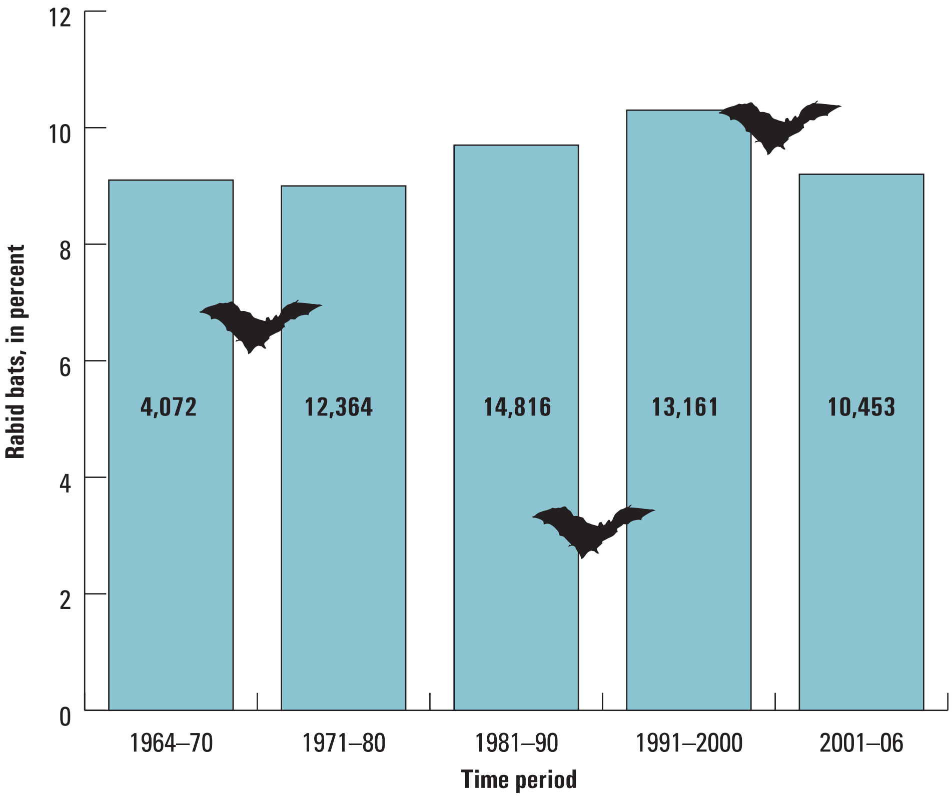


Figure 5. Percentage of rabies-suspect bats identified as rabid in the United States from 1964 to 2006. The first documented bat rabies case in humans was identified in 1953; bat rabies surveillance records are unsatisfactory for 1954–63. (Bold numbers indicate the number of bats tested during the indicated time period. Compiled from U.S. Centers for Disease Control and Prevention data.)

Species Susceptibility

It has long been assumed that all mammals are susceptible to rabies infection, a view that may apply in varying degrees to the other lyssaviruses as more is learned about them. No gross lesions aid in the identification of lyssavirus infections, so diagnosis of living or dead untested subjects is tentative and based on history, which usually includes reports of behavior that is not specific to the disease. Rabies virus is known to be maintained within two reservoir host mammal groups, carnivores and bats, and carnivores host virus variants that differ considerably from those hosted by bats (Constantine, 1967a). Rabies and other lyssavirus infections have been reported from 114 bat species (Appendixes B and D), including 33 in the USA (Appendix A; Table 3). Australia has the fewest number of bat species (five documented) with lyssavirus infections; the numbers of infected species for Asia, Africa, and Europe also are low (Appendix D; Fig. 6). The lyssaviruses identified from infected bats represent 10 (including rabies) of the 11 currently named or putative genotypes for this virus group, and several of the lyssaviruses from bats remain unclassified (Table 1). Thus, there is adequate reason to regard all lyssaviruses to be potentially as deadly as classical rabies.

Table 3. Bat families in the USA reported with bat rabies.

Family	Food habits	Number of infected species
Phyllostomidae	Omnivorous [1]	1
Mormoopidae	Insectivorous	1
Molossidae	Insectivorous	4
Vespertilionidae	Insectivorous	27

[1] Members of this diverse family of neotropical bats feed upon insects, small vertebrates, blood, fruit, nectar, and pollen.

The results of exploratory rabies transmission experiments provided the first indication of the existence of viral variants. These experiments demonstrated that the spectrum of carnivores susceptible to infection differed according to the bat species origin of rabies virus, as did incubation periods, duration of illness, and morbid behavior (Constantine, 1967a). Maladaptations, such as the death of the host before the virus can reach the saliva for transmission, reveal why infections of new, unadapted host species may, in effect, be dead end.

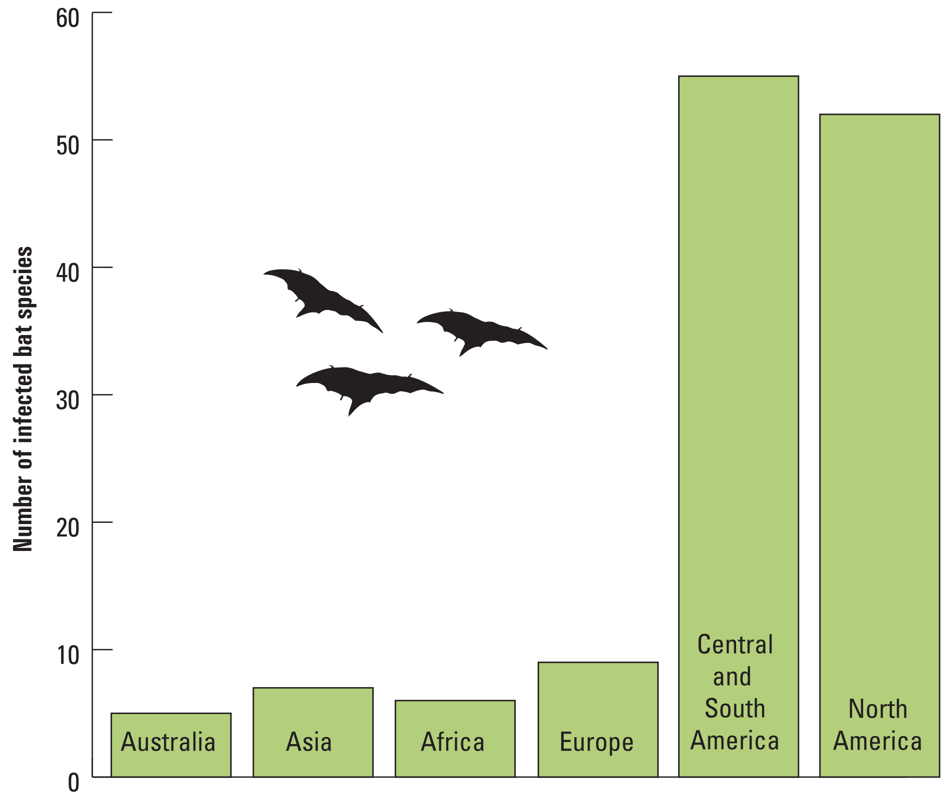


Figure 6. Number of rabies- and other lyssavirus-infected bat species by continent.

Human Infections

Each year as many as 100,000 people globally may die of rabies (Rupprecht and others, 1995), and ten million people take antirabies treatment (Goswami and others, 2005). Carnivores, principally dogs, are the **vectors** for the great majority of rabies transmissions to people in developing areas. In Latin America, thousands of people must have died, and hundreds continue to perish due to vampire bat-borne rabies, but case reports are lacking from some countries, particularly from their remote regions. Due to competition for limited resources for research of the causes of human mortality, vampire bat rabies infection in humans, especially those living in inaccessible areas, did not receive adequate attention until recently (Navarro Vela, 2001; Takoaka and Omoto, 2001; Vargas Pino, 2001). Reports of human rabies due to bats other than vampires are difficult to discern because of local inability to differentiate vampire bats from any of the great variety of bat species in Latin America.

The recognition of human lyssavirus infections of bat origin exists to varying degrees in developed countries. The existence of bat rabies and associated human mortality in North America north of Mexico was unknown prior to the 1950s. Between 1951 and 2006, 51 recognized human rabies cases in the USA and Canada were determined to be of insectivorous bat origin (Table 4), and there is some evidence that bat rabies existed before 1951 in these countries (Christensen, 1946; Constantine, 1967b). This revelation of bat-associated human rabies mortality as a result of public health investigations has been mirrored elsewhere for other lyssaviruses (Table 5).

The onset of clinical disease in humans infected by rabies virus nearly always results in death (Box 2). Exceptions are so noteworthy as to be the subject for scientific reports (Hattwick and others, 1972; Porras and others, 1976; Willoughby and others, 2005; Box 3). Examples of the course of disease in humans infected by bat lyssaviruses (Appendix E) illustrate the consequences of those infections and the variability in incubation time between exposure and the onset of clinical disease (Table 6).

The Course of Bat Rabies in Humans

Box 2

Rabies in humans is characterized by a variable incubation period, usually from 1 to 3 months, but ranging from 10 days to a year or more. The disease then generally develops in three phases: **prodromal**, excitatory, and paralytic (Fishbein, 1991). Prodromal signs last from 2 to 10 days, are nonspecific, and include slight fever, malaise, headache, nausea, dilation of the pupils, sore throat, anxiety, irritability, and perhaps sensitivity to wind, bright light, and noise. More significant are abnormal sensations such as pain, burning, cold, and itching or tingling near the site of virus entry, such as a bite.

The excitatory phase, present in 80 percent of cases, may be absent, rapidly transitory, last 1 week, or continue until death. During this phase, victims experience increasing anxiety, apprehension, and **melancholia**. Muscles around the virus entry site may weaken. Eyes may undergo unusual or uncoordinated movements, pupils may undergo asymmetric dilation or constriction, and eye **corneas** may be insensitive to touch. Facial muscles may weaken and hoarseness develops. Other signs can be alterations in heart rate and intensity, respiratory rate and depth, urinary retention followed by overflow incontinence, and constipation. The classical manifestation of rabies in humans is hydrophobia, when upon attempts to swallow liquid, the victim forcefully expels it due to the involuntary contraction of the muscles involved in swallowing and respiration. This reaction is subsequently repeated if the victim is provoked by the sight or sound of liquids. The convulsive attack may cause death through choking and failure to breathe. The victim may suddenly die from respiratory arrest or death may be preceded by coma.

Paralysis, which predominates in 20 percent of cases, may precede death by 1–4 weeks. Swallowing is possible but becomes difficult. A general **flaccid paralysis** develops. Apathy progresses to stupor, followed by coma, peripheral vascular collapse, and death.

Table 4. Insectivorous bat origins of human rabies infections recognized in the USA and Canada from 1951 to 2006.

Bat species	Family	Number of bat carcasses identified taxonomically	Number of lyssaviruses identified to the variant level	Total number of bats involved in human rabies infections
Brazilian free-tailed bat	Molossidae	7	10	10
Big brown bat	Vespertilionidae	2	[1] 3	3
California myotis	Vespertilionidae	1	1	1
Myotis sp.	Vespertilionidae	0	1	1
Silver-haired bat	Vespertilionidae	1	11	11
Tricolored bat	Vespertilionidae	0	17	17
Totals		**11**	**43**	[2] **51**

[1] Variants were an Ef (Big brown bat)-associated, a Ps (Tricolored bat)-associated, and an undetermined variant.

[2] Total includes eight bats for which neither the bat taxonomic identity nor the virus variant were determined.

Box 3 Human Survival of Clinical Rabies—An Exception to the Rule

Cases of patients surviving rabies infection after the appearance of clinical signs, without preexposure vaccination or postexposure prophylaxis or both, are rare. However, two cases of patients surviving clinical rabies are well documented. The first case was a 6-year-old boy in Ohio (Hattwick and others, 1972), and the second was a 15-year-old girl in Wisconsin (Willoughby, Jr., and others, 2005). Both patients were exposed to rabies through bat bites. In each case, aggressive supportive treatment was given to avoid or decrease the known or anticipated ravages of the disease. The reasons for the success of the administered treatments are not fully understood, but the positive outcomes offer incentives for continuing research efforts.

Case 1

A 6-year-old boy was bitten on his left thumb by a rabid big brown bat on October 10, 1970, while he was asleep in his family's farmhouse near Wilshire, Ohio. Four days later, a 14-day course of rabies vaccine was begun, but no antirabies serum was given (Table 1). Recovery was complete 6 months after the onset of symptoms.

The physicians (Hattwick and others, 1972) suggested that the rabies strain in this case may have been less virulent for humans than other strains, however that hypothesis was not pursued. Rabies variants from big brown bats have been shown to possess extremely different abilities to cause infection in animals (Bell and others, 1962; Constantine and others, 1968b), and geographically distinct rabies variants from this species are known in the United States (De Mattos, C.C. and others, 2001). For example, a bat identified as a big brown bat transmitted lethal rabies by bite to a woman in Maryland (Barnhart and others, 1976), but the rabies variant proved to be associated with the tricolored bat (Messenger and others, 2002). Alternately, an unidentified bat transmitted lethal rabies by bite to a man in Washington in 1997, and the rabies variant was identified as originating from a big brown bat (Geyer and others, 1997).

Case history 1.

Day of symptoms	Symptoms/treatment
1	Neck pain developed 2 days following the vaccine series (60 days after the victim was bitten by the bat).
5	High fever, appetite loss, vomiting, and dizziness, but alert and cooperative.
11	Pain in head and limbs, became lethargic, writing and walking were difficult.
13	Speech problems, uncooperative and bizarre behavior, bit and chewed on his saliva collection tube, weakness, partial paralysis, and seizures of the left side of the face and left limbs.
15	Coma, heart rhythm irregularities, and seizures. Aggressive treatment continued to prevent oxygen deprivation and intracranial hypertension. Excess cerebrospinal fluid removed from within the brain.
22	Coma ended and recovery began.

Case 2

A more recent case of survival also involved a bat, but the species is unknown. In October 2004, in Fond du Lac, Wisconsin, a 15-year-old girl was bitten on her left index finger by a bat that she picked up and released outside after it had fallen from flight while it was inside a church. Nobody considered a potential rabies danger, thus rabies prophylaxis was not administered. The first symptoms appeared about 1 month later, and the patient was discharged from the hospital 80 days following the onset of symptoms (Table 2). Rehabilitation following release from the hospital contributed to this success story. A tutor helped the victim finish her sophomore year of high school so that she could rejoin her classmates in the fall. Physical therapy helped her to overcome speech problems, weakness in her left hand and foot, and abnormal movements in her arms and hands. The victim entered college as an 18-year-old freshman in the fall of 2007. She regrets that none of the 10 other rabies patients subsequently administered the same or similar treatment survived, but she continues her life with energy and enthusiasm. She is an aspiring wildlife conservationist, and she still loves animals, including bats.

Case history 2.

Day of symptoms	Symptoms/treatment
1	Fatigue, tingling, and numbness of the left hand about 1 month after the victim was bitten by a bat.
3	Unsteadiness, double vision, nausea, and vomiting, but no fever.
5	Fever of 101.8 °F (38.8°C), slurred speech, involuntary eye movements, and tremors of the left arm.
6	Bat bite revealed, patient transferred to the Medical College of Wisconsin with a fever of 100.8°F (38.2°C), muscular twitching, incoordination, difficulty speaking, tremors in the left arm, dulled alertness, and hypersalivation. A tracheal breathing tube was installed. Because rabies signs had already developed, rabies vaccine or antirabies serum were not administered.
7 to 34	Partial paralysis and numbness due to sensory nerve dysfunctions. Extensive supportive treatment administered, including mechanical breathing, heart monitoring and treatment, intracranial hypertension control, antiviral drugs, and a drug-induced coma permitting the patient's rabies antibodies to increase and destroy the virus. After 7 days of coma, sedation medications were discontinued, and the patient became increasingly alert.
35	Patient removed from isolation and started on a rehabilitation program.
80	Patient discharged to her home.

Coma and Intervention

Although both human rabies survivors experienced coma, a natural and often terminal development in clinical rabies, the medical personnel of the first case merely acknowledged its existence whereas those in the second case induced coma with drugs. The latter authors (Willoughby, Jr., and others, 2005) said it was not clear if the induced coma played a role in the victim's recovery, but they recommended that their updated protocol and future updates (Medical College of Wisconsin, 2007) be followed in the treatment of subsequent patients. A focus for consideration is control of the patient's body temperature.

Table 5. Human nonrabies lyssaviral infections reported in Africa, Asia, Australia, and Europe.

[ABL, Australian bat lyssavirus; EBL, European bat lyssavirus]

Location	Year	Source of infection [1]	Number of human cases	Lyssavirus species	Reference
Australia	1996	Bat	1	ABL	Allworth and others, 1996.
Australia	1997	Bat	1	ABL	Hanna and others, 2000.
China	2002	Bat	1	Rabies-like [2]	Tang and others, 2005.
Finland	1985	Bat	1	EBL-2	Lumio and others, 1986.
India	1954	Bat	1	Rabies-like [2]	Veeraraghavan, 1955.
Kenya	2007	Bat	1	Duvenhage	van Thiel and others, 2008.
Nigeria	1968	Unknown	1	Mokola	Familusi and others, 1972.
Nigeria	1971	Unknown	1	Mokola	Familusi and Moore, 1972.
Russia	1985	Bat	1	EBL-1	Botvinkin and others, 2005.
Scotland	2002	Bat	1	EBL-2	Fooks and others, 2002.
South Africa	1970	Bat	1	Duvenhage	Meredith and others, 1971.
South Africa	2006	Bat	1	Duvenhage	Paweska and others, 2006.
Ukraine	1977	Bat	1	Rabies-like [2]	Botvinkin and others, 2005.
Ukraine	2002	Bat	1	Rabies-like [2]	Botvinkin and others, 2005.

[1] Bat species not reported.

[2] Untyped lyssaviruses causing rabies-like clinical signs.

Bat Infections

Studies of rabies in North American insect-eating bats reveal that **incubation periods** can be from 21 days to at least 209 days, and the duration of the disease can last from less than 1 day to 20 days. Most important, however, is the knowledge that individual bats have transmitted the virus by bite as early as 12 days before the appearance of **clinical signs** and 24 days before the death of the bat (Constantine, 1994). In either situation, a bitten person could develop clinical disease or be dead of rabies before clinical signs appear in the biting bat, a sobering prospect for persons who prefer to spare the life of a biting bat. Worse yet, if the bat becomes chilled, and thus lethargic or **torpid**, all of these periods become extended. For example, some bats are known to awaken from **hibernation** in spring, whereupon they resume development of rabies infection that has been placed on hold all winter (Constantine, 1967a; Box 4).

Paralytic rather than **furious rabies** appears to be characteristic of rabies in most infected bats, but there are disturbing exceptions. Infected insectivorous bats display neither external nor internal gross lesions nor clinical signs specific enough to permit a diagnosis prior to laboratory tests performed on brain tissue. They may display a variety of nonspecific clinical signs that change as the disease progresses or in response to environmental influences. Basically the bat may be expected to suffer nervous system disorders that make it overly responsive to sensory stimuli, such as touch, and that elicit retaliatory bites, tremors, and perhaps wing flapping. However, these responses are not diagnostic, because the approach of persons or animals can elicit similar behavior in healthy bats. Progressive paralysis of infected bats can increase irritability and biting of nearby objects. Such biting may also be used as an aid in crawling or climbing as paralysis disrupts coordination. Developing paralysis can oblige flying bats to alight on any elevated object, even a standing person, rather than land on the ground. Thus, bats found in unusual places may be infected. Flight problems decrease the bat's ability or efforts to secure food and water, leading to attendant weight loss and dehydration; captive bats simply cease to eat. If an infected bat does not fall to earth during flight, it may finally die in its shelter. In either situ-

Table 6. Examples of incubation periods and times to death relating to human mortalities from bat-associated lyssavirus exposure.

[See appendix E for more detailed descriptions of the nine cases below]

Case[1]	Exposure location	Day of onset of symptoms after exposure	Day of death following onset of symptons	Comments
1	South America	27 days	9	Victim bitten on toe while sleeping; bat seen flying from foot when victim awoke.
2	North America	16 days	9	Victim bitten on forearm when bat picked up from ground.
3	North America	About 6 weeks	4	Airborne exposure in cave occupied by millions of bats.
4	North America	26 days	12	Victim bitten on finger when bat was rescued from attack by dogs; dogs potentially exposed.
5	North America	21 days	7	Victim bitten on ear while sleeping; bite awoke victim, cat ate bat; cat potentially exposed.
6	Europe	51 days	11	Victim bitten by abnormally acting bat that was then released.
7	Africa	About 1 month	4	Victim awakened by bat bite on lip.
8	India	About 11 weeks	[2] 5	Victim bitten on forearm when bat was picked up from ground.
9	Australia	Unknown	16	Victim cared for fruit bats.

[1] Case 1, Hurst and Pawan, 1932; Case 2, Sulkin and Greve, 1954; Case 3, Irons and others., 1957; Case 4, Humphrey and others, 1960; Case 5, Humphrey and others, 1960; Case 6, Lumio and others, 1986; Case 7, Meredith and others, 1971; Case 8, Veeraraghavan, 1955; Case 9, Allworth and others, 1996.

[2] May be longer, because the day of the onset of symptoms was not recorded.

ation, lack of activity can result in lethargy and consequent life extension before death (Constantine, 1967a; Sadler and Enright, 1959).

Rabies in experimentally infected vampire bats resembles the previously described infections in insect-eating bats in reference to the clinical disease, incubation period, illness period, and periods when virus can be detected in saliva (Moreno and Baer, 1980). This contrasts with early reports that vampire bats could be healthy carriers and excretors of rabies virus in saliva (Torres and de Queiroz Lima, 1935; Pawan, 1936). However, those early investigators may have mistaken as rabies one of a number of other viruses that can chronically infect bat **salivary glands** (Constantine, 1970; Constantine, 1988b). Another important characteristic of vampire bats is that, unlike most **temperate zone** bats, the tropical vampire bats are not physiologically able to lower their body temperatures to become lethargic or dormant, which would defer viral disease development (Lyman and Wimsatt, 1966).

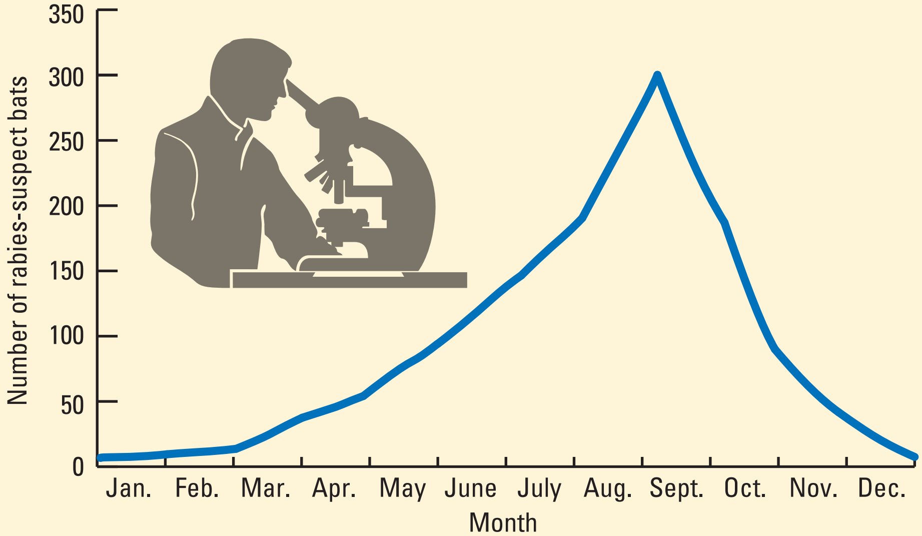
Most infective bites from insectivorous bats are inflicted in a manner similar to bites inflicted by healthy bats for self-defense, such as when a bat is caught by a person or an animal. Rarely, however, some rabid bats, including insect eaters, are known to attack people, most often during daytime. Furious daytime attacks on people and animals by rabid common vampire bats have long been known during outbreaks in Latin America (Haupt and Rehaag, 1921; Torres and de Queiroz Lima, 1935; Pawan, 1936). Noise produced by or associated with the victim evidently can precipitate attacks (Constantine, unpub. data). Such attacks, like one experienced by the author, are known to be direct and quick, unlike the erratic flight of bats in pursuit of insects. Similarly, lyssavirus-infected black flying foxes of Australia are known to attack other bats repeatedly (Mackenzie, 1999). Unprovoked attacks by bats are clearly suggestive of rabies, but they are difficult to differentiate from events described by frightened people who think they are under attack by healthy bats that, in reality, are in pursuit of nearby flying insects.

Human perceptions of abnormal behavior by bats are not always correct and often result in healthy bats being mistaken as ill. Rather than being infected, the bats may be lethargic or dormant when at rest in a cool place. In addition, young bats may not yet be able to fly, or bats injured from cat attacks or other causes may appear partially paralyzed. Species that take shelter in the soft foliage of trees, such as hoary bats, sometimes are attacked by **birds** and fall to earth, where their tender wings suffer abrasions. These abrasions may cause the bats to react with a hissing sound and to extend their wings and thrash about in an effort to become airborne. This behavior occurs whether or not the bat is infected with rabies.

Box 4 Seasonal Bat Behavior and Disease Transmission

Most North American bat species live in temperate zones and are **heterothermous**, in that when a bat is inactive or sleeping its body temperature corresponds to that of the environment, similar to what is observed in cold-blooded (**poikilothermous**) **reptiles** and **amphibians**. When a heterothermous bat is active, however, its body temperature is regulated to a uniform warm level like that of most warm-blooded (**homoiothermous**) mammals and birds. Thus, when the environmental temperature decreases, heterothermous bats become cold and eventually lethargic or dormant when at rest, similar to a hibernating state that results in conservation of energy. Their flying insect food responds similarly to cold weather and does not fly. Many of these bats, the long-legged myotis for example, hibernate in winter, whereas others migrate to warm areas. Because most North American bat species either migrate to warmer climates or are inactive in cooler areas during cooler months, bat rabies similarly disappears during the winter. Accordingly, cases of bat rabies in the USA routinely start appearing in spring, increase until early fall, and decrease thereafter. North America's seasonal cycle of bat rabies has been repeated in part and with similar results in Latin America, Europe, Asia, Africa, and Australia, but seasonal patterns are less pronounced toward the equator.

Long-legged myotis. (D.G. Constantine)



Submissions of bats suspected of having rabies, by month (reproduced from Blanton and others, 2007).


California leaf-nosed bat. (D.G. Constantine)

A smaller number of temperate North American bat species are full-time homoiothermous mammals. These bats cannot hibernate and must remain in a warm environment at all times. The California leaf-nosed bat, whose warm geographic range extends from Mexico into southern California and Arizona, does not migrate southward in winter and often inhabits geothermally warmed mine tunnels or caves. It selects warmer sites for shelter during winter, often within the same underground lair, and it flies outside to capture its insect prey as the weather allows.


Brazilian free-tailed bat. (D.G. Constantine)

The Brazilian free-tailed bat, found in warm parts of North and South America, is intermediate between the homoiothermous and heterothermous bats. Although its body temperature decreases if it is inactive during short cold periods, it cannot undergo true prolonged hibernation. Instead, it migrates to relatively warm areas for winter, where the bats and their flying insect food both remain active.

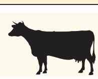
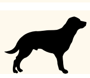
Infections in Other Species

In addition to direct exposures of humans to rabid bats, other animals, principally carnivores, may become infected or contaminated by rabid bats and consequently become additional sources for infection (Table 7). Experiments have demonstrated that domestic and wild carnivores are among the species susceptible to rabies variants of North American insectivorous bat origin, although variants differ in their degrees of infectivity for various carnivore species (Constantine, 1966a; Constantine, 1966b; Constantine, 1966c; Constantine and Woodall, 1966; Constantine, 1967a; Constantine, 1967b; Constantine and others, 1988a; Constantine and others, 1988b). Laboratory mice have been experimentally infected by bites of North American insectivorous bats (Bell and others, 1962). In addition, in 2006 following a public exhibition attended by approximately 150,000 people, a horse was diagnosed postmortem to have been infected with a rabies variant associated with big brown bats (Blanton and others, 2007). As a result, a health alert was issued by the state health department and 53 people who had attended the exhibition were consulted about potential rabies exposure. Some carnivores and other species are also known to be susceptible to other lyssaviruses (Table 1).

Figure 7. Circular pattern of earth excavation (dark area of ground behind calf (indicated by an arrow) resulting from confined body movement associated with posterior paralysis in a rabies-infected Zebu. (G.C. Mitchell)

Vampire bat-transmitted rabies can kill and decimate herds of cattle as well as destroy horses, **mules, donkeys, burros**, goats, sheep, pigs, dogs, and **poultry**. Poultry, however, often soon die from **exsanguination** rather than rabies (Greenhall, 1988). After an incubation period of about 1 to 2 months, the disease kills cattle within several days to a week. Initially the animal is restless, perhaps excitable, and loses its appetite. The next day, its rear legs tremble and are uncoordinated due to developing paralysis, and it salivates profusely because of difficulty in swallowing. Some animals, especially **Zebu** cattle, may charge people, but the disease is primarily paralytic rather than furious. By the third day the animal is constipated, eventually falls onto its side, and cannot rise. On about the fourth day, posterior paralysis is complete, but attempted running with the forelegs can result in circular movement and consequent circular earth excavation (Fig. 7). Death follows in the next day or two (Baer, 1991).

Table 7. Examples of nonbat species infected by rabid bats.

Species infected	Relative occurrence	Natural or laboratory infection	Comments
Cattle 	Common	Natural and laboratory infection	Major vampire bat problem in Latin America.
Cats 	Occasional	Natural and laboratory infection	Increasing problem, presumably by bat bite or bat ingestion.
Dogs 	Rare	Natural and laboratory infection	Presumably by bat bite or bat ingestion.
Foxes 	Rare	Natural and laboratory infection	By bat bite, bat ingestion, or aerosols in congested free-tailed bat caves.
Skunks 	Rare	Natural and laboratory infection	Presumably by bat bite or bat ingestion.
Coyotes 	Rare	Laboratory infection and presumed in nature	By bat bite, bat ingestion, or aerosols in congested free-tailed bat caves.
Laboratory mice 	Only in laboratory	Laboratory infection	By bat bite.

Obtaining a Diagnosis

A bat that is suspected of being infected with a lyssavirus must be euthanized and its brain tested in a laboratory to obtain a diagnosis. Standard tests for rabies virus suffice for lyssaviruses known to exist in the Americas or Australia, but special tests at regional disease diagnostic laboratories may be necessary to identify lyssaviruses found in Europe, Asia, Africa (Table 1), and perhaps elsewhere.

Because of the consequences for a human infection, the handling of bats merits precautionary measures. Local health departments generally provide directions to the public regarding submission of bats for laboratory diagnosis. Heavy leather work gloves prevent bites from most live insectivorous bats, and rubber gloves prevent skin contamination from the saliva or tissue fluids of dead bats. The bats often will be retrieved by animal control personnel. Dead bats should be double bagged and kept cold or frozen, even if they are decomposed or partially eaten. It is important to keep the dead bats cold or frozen to prevent further decomposition that may render test results unreliable, which would force medical personnel to decide that the bat was infected and to initiate appropriate lifesaving precautions for individuals known to have been exposed to the bat.

Complete histories that accompany submitted bats facilitate the rapid notification of persons-at-risk, the initiation of timely lifesaving medical management, and disease management involving relevant pets. Pertinent information often is not sought until after the bat has been determined to have been infected, thus causing the delay of lifesaving measures while information is obtained. Histories are most informative when they reconstruct the trail of events since the bat was first observed, including the kinds of known and potential exposures (bites, scratches, saliva, tissue fluids, etc); dates; places; the names, addresses, and telephone numbers of associated persons and animal owners; and known as well as potential pet or other animal contacts.

Disease Ecology

The ecology of bat rabies and other lyssavirus infections is closely associated with bat ecology, including bat feeding strategies (Box 5) and the dynamics of infection within various bat species. Thus, those factors provide the focus for this section on Disease Ecology, along with differences in global virus transmission in relation to vampire bats or to other bats. Consideration is also given to the environmental persistence of lyssaviruses and their hosts.

Bat Activity and Disease Patterns

Bat lyssavirus is evident where and when bats are present and physiologically active (rather than in hibernation), which coincides with the availability of bat food. Most information on this subject is derived from studies in the temperate and tropical areas of America, with evidence of comparable patterns in these zones globally. Bats are present and active in temperate areas during warm seasons, when their flying insect food is available, and correspondingly, bat infection is also evident at these times. As the cold season approaches, evidence of both insects and bats decreases and eventually disappears, as do cases of bat lyssavirus. During this period, some bat species migrate to warmer areas, where insects are available. Other species retire to cold sites like caves to hibernate instead of migrating (Fig. 8). In contrast, bat food, such as insects and fruit, is available during all seasons in tropical areas, and bats and bat infections may be evident continuously in those areas.

Figure 8. Townsend's big-eared bats awakening from hibernation. The ears of some bats are still folded beneath their folded wings, in typical hibernation position. (D.G. Constantine)

Box 5 Bats—Diverse Mammals with Diverse Diets

Bats are distributed globally to the limits of tree growth and divided into 1,116 species (Simmons, 2005). Different groups or species of bats exhibit specialized dietary preferences. Bats in temperate zones are less numerous and diverse than those in tropical zones. Thus, while insectivorous bats are most common in temperate regions, the greater availability and variety of dietary items near the equator supports a diversity of food choices and food specializations among tropical bat species, a few of which are discussed below.

Diadem leaf-nosed bat (D.G. Constantine)

The diadem leaf-nosed bat of northern Australia hangs in ambush from a tree branch, ready to fly out and capture passing flying insects. Some insectivorous bats specialize in eating aquatic insects, which they detect and gaff with elongated claws on large feet as the insects break the water surface. Similarly, other bats, such as the greater bulldog bat, gaff small fish to either supplement or replace their insect diet. Some bats snatch earthbound insects, sometimes capturing lizards as well. Other bats take insects that feed on ripe fruit, which the bats may also consume.

Queensland tube-nosed fruit bat. (D.G. Constantine)

The Queensland tube-nosed fruit bat of northern Australia feeds on the fruits and blossoms of native trees. This bat's tubular nostrils may function as snorkels when its muzzle is immersed in mushy fruit pulp. Because they do not have to chase and kill prey to survive, fruit bats exhibit a placid demeanor and seem to expect courteous treatment from people in return. For example, the pictured tube-nosed bat immediately accepted and consumed an offered banana, forgoing the opportunity to flee. Similar behavior has also been observed among other neotropical fruit bats.

Fringe-lipped bat. (D.G. Constantine)

The fringe-lipped bat, the pictured example observed in a Venezuelan cave, eats insects, lizards, and frogs, grabbing its prey between its jaws while in flight. It is attracted to frogs by their calls, recognizing frog species by their sounds and thus bypassing poisonous frogs.


Greater spear-nosed bat. (D.G. Constantine)

The greater spear-nosed bat is **omnivorous**, eating insects, smaller bats, mice, birds, and fruit. The pictured bat, netted in Trinidad, shared the author's dinner the day it was captured, eating filet mignon and fruit salad.

The common vampire bat, the pictured example captured in Trinidad, is **sanguivorous** and consumes only blood. Literally bloodthirsty, it will die if it does not feed for 3 nights. Fearless when under attack, vampire bats deftly escape from potential predators, a reaction that can be unnerving to a human trying to outwit a single bat, to say nothing of an encounter with a dozen or more. Regardless of the size disparity, vampire bats view humans as a source of nourishment. The first vampire that the author observed was on all fours, with its wings folded to serve as forelegs, staring at him from a ledge near the ceiling of a Mexican cave and trying to determine its distance to the potential human prey by doing "push-ups" and moving its head from side-to-side, similar to an owl's head movements during hunting. Several nights later another vampire bat, caught in the author's **harp trap** (Constantine, 1958) as it tried to enter a calf pen in search of a meal, likewise stared at the author, calculating its distance to him from within its cage. The vampire bat's predatory nature shows courage, determination, and rapid responses when it must avoid retaliatory attacks, such as repeated kicks when it tries to obtain blood from the hind feet of cattle. Vampires are adept at avoiding kicks by jumping out of the way, only to swiftly return.


Common vampire bat. (D.G. Constantine)

A vampire bat caged with a rat will relentlessly pursue the rat as prey and almost invariably triumph, even "boxing" the rat with its folded wings to ward off retaliatory charges. Similarly, when caged with a large snake intent on eating the bat, the vampire is capable of repeatedly avoiding strikes and persistently holding its course until able to obtain its blood meal from the nose of the seemingly hypnotized snake (Greenhall, 1988). Thus, the impression is fostered that the bat is endowed with the supernatural powers of the fictitious Dracula (Stoker, 1897).

The most effective way to determine if infected bats exist in an area is to test clinically ill and dead bats. This type of surveillance for lyssavirus infections is often required for protection of the public health. Although the **prevalence** of infection among clinically ill bats varies from species to species in the USA, it averages 10 percent, which is similar to the 8 percent prevalence reported in Europe. To find at least one infected bat, one must test a minimum of 22, 29, or 44 clinically ill bats for statistically reliable results at confidence levels of 90, 95, or 99 percent, respectively (Constantine, 1994).

Studies of some bats indicate that they undergo population fluctuations in response to mortality caused by lyssavirus infection, similar to the occurrence of the infection in carnivores such as foxes and skunks (Constantine, unpub. data). Mortality decreases the population, and accordingly, evidence of subsequent disease until the population increases to a density that again supports lyssavirus transmission through increased frequency of contact. Increased rainfall can hasten population growth by providing greater plant growth to support the development of bat food, such as insects, and thus the greater survival of bats. Some migratory bats will forsake areas of drought for more suitable places. At the other extreme, however, atypically prolonged rainfall retards the flight of both insects and bats and is known to cause mass starvation of some bat species (Constantine, 1982a).

Temperature and Rabies Virus Virulence

Temperature can be critical in the manifestation or control of diseases, including rabies. The **hypothermia** of hibernation increases the resistance of an animal host to various viral, bacterial, and metazoan parasites. In many instances, disease is prevented or diminished. In other instances, disease development is deferred during hypothermia and resumes when the host awakens. In addition, viruses usually cannot replicate at higher temperatures, and fever in the infected host serves to depress viral development. However, certain highly pathogenic virus strains have adapted to this condition and are able to replicate at higher temperatures. Lower body temperatures may favor less virulent rabies virus strains. The seasonal differences in the body temperatures of heterothermic bats may account for some virulence differences observed among the rabies virus variants from different bat species (Constantine, 1967a; Constantine,1970).

How Colonial Bats Avoid Extinction by Lyssaviruses

It would seem that highly colonial animals, such as many bat species, would be eliminated quickly after a lyssavirus enters the population, but multimillion-bat colonies persist in the presence of the disease. Studies of rabies in huge populations of Brazilian free-tailed bats in caves of the southwestern USA and Mexico provide some insight into this question (Constantine and others, 1988a). In essence, **maternal antibody** provides a protective barrier or **passive immunity** against disease upon virus exposure within the colonies. Subsequent virus exposure then stimulates the immune system to provide protective antibody or acquired immunity for the long-term protection of exposed bats (Box 6).

Paralytic and Furious Disease Courses

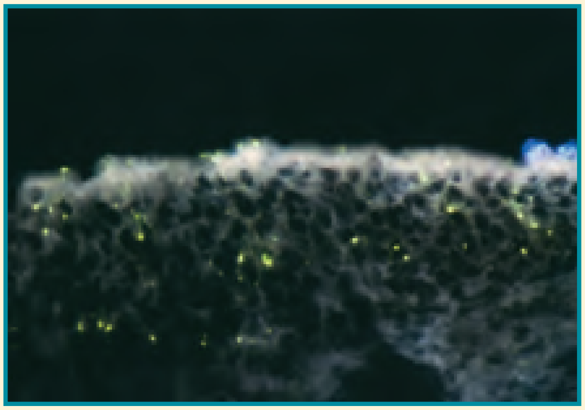
The author's early experiences with bats and bat rabies in North America indicated that rabid bats experienced only the paralytic form of the disease without obvious aggressiveness or furiousness. For example, he and coworkers spent the equivalent of many years in and about caves occupied by millions of Brazilian free-tailed bats and were never attacked, although one of every 200 bats was infected (Fig. 9). In addition, none of the thousands of bats of other colonial bat species attacked under similar circumstances. Logic suggested that sufficient biting or other forms of transmission had occurred normally and frequently enough among these crowded animals to have rendered the furious form of rabies relatively superfluous and perhaps obsolete as a viral survival mechanism.

However, lyssavirus-infected bats do attack. Initial reports of attacks by flying rabid bats were limited to certain species that live as solitary individuals. These included the more diminutive of North American bats, primarily the canyon bat (Fig. 10), and, less often, the western small-footed myotis (Fig. 11) and the California myotis (Fig. 12) (Constantine, 1967a). It was suspected that deliberate attacks by these small solitary bats on **conspecific** bats had been retained as a necessary viral survival mechanism. Eventually, however, attacks on people by individual rabid bats of various species, including Brazilian free-tailed bats and other colonial bats, were documented. Fortunately, such attacks are rare events that are committed by individual rabid bats separated from colonies that otherwise would seem to dominate their interest. Thus, unwary investigators were likely spared attacks because they could not compete with the noisy bat colonies for the attention of any rabid bats primed for attack.

Immunity to Lyssaviruses in Colonial Bats

Box 6

Studies of rabies in huge populations of Brazilian free-tailed bats in caves of the southwestern USA and Mexico revealed that rabies infection is present in about 0.5 percent or 1 of every 200 of the mature bats (Constantine and others, 1968a). Disease transmission by infective saliva was possible from bites, licking of saliva into wounds or **mucosal surfaces**, or contamination by or inhalation of cave air charged with droplets of saliva expelled by the chattering bats (Constantine, 1967a; Constantine, 1967b). As many as 80 percent of the bats examined possessed recognizable **blood serum** antibodies against the virus. Colonial bats develop life-long immunity to rabies virus by two mechanisms. Unborn and suckling bats receive a temporarily effective dose of antibodies by way of the **placenta** and milk (**passive immunity**), but this immunity is typically lost 6 to 10 weeks following birth (Constantine and others, 1968a). Many young bats, while they are still temporarily immune, are also likely exposed to virus, which they resist by passive immunity, but against which they consequently developed long-lasting antibodies (**active immunity**). Such bats would be expected to respond to future viral exposures as if they were receiving booster doses of rabies vaccine. Young bats killed by rabies within the colonies were presumably produced by non-immune mothers. This scenario provides a mechanism for these populations to survive in the presence of rabies virus. The virus "immunizes" most of the population, but it still claims sufficient victims to maintain disease within the colony so that the virus persists.



The nasal mucosa may be a site of rabies entry and exit from victims in some highly congested bat caves. This 2-micron section of nasal mucosa from a symptomatic, immature Brazilian free-tailed bat (*Tadarida brasiliensis*) from the Frio Cave, Uvalde County, Texas, was stained with fluorescent dye that indicates the presence of rabies antigen, shown by the apple green areas.

Figure 9. Brazilian free-tailed bats attempting to find roosting space among a dense colony of cohorts on a cave ceiling (bat density equals approximately 300 bats per square foot). (D.G. Constantine)

Figure 10. Canyon bat in flight. (D.G. Constantine)

Figure 11. Western small-footed myotis bat in flight. (D.G. Constantine)

Figure 12. California myotis bat in flight. (D.G. Constantine)

Figure 13. Big brown bat in flight. (D.G. Constantine)

Viral and Host Species Diversity

Current information suggests that each species of lyssavirus may be divisible into several or more strains called variants. Each variant is maintained within populations of a particular reservoir host species to which it is adapted. Typically, these hosts are isolated by ecologic, anatomic, and social factors from other host species. Further isolation is afforded to viral variants harbored within sedentary, nonmigratory host species. Recent studies indicate that some sedentary reservoir host species populations are divisible into different **DNA**-identifiable host subpopulations that occupy different extensive, although often contiguous, geographic areas. Thus, these subpopulations provide conditions of isolation that favor the development of unique viral variants. For example, such a geographic correlation between nonmigratory big brown bat (Fig. 13) populations and the distributions of the rabies virus variants they maintain has been observed in the USA (De Mattos C.C. and others, 2001). The nonmigratory common vampire bat rabies virus is similarly divided into at least three geographically distinct variants (De Mattos, C.A. and others, 2001). In contrast, the Brazilian free-tailed bat, whose migratory habits conflict with population isolation and differentiation (McCracken and others, 1994), harbors fewer and less contrasting variants (Smith, 1996).

Although the association of a given virus variant with a particular animal host species can be useful for tracing the origin of infection in atypical victims, such as humans, it cannot rule out **intermediate hosts**. For example, cats that chew infected bats may subsequently transmit the virus to people, either promptly by mechanical transmission or perhaps later if the cat develops rabies. However, the relatively rabies-resistant cat may not become infected, eliminating it as a suspect intermediate host (Constantine, 1967a; Bell and Moore, 1971). Thus, these early studies indicated that rabies viruses recovered from various bat species differed in their abilities to infect or produce (or both) particular pathological responses in a given spectrum of wild carnivore or laboratory mammal species. These studies foreshadowed later serological methods followed by protein- and RNA-based analyses that now are used to delineate virus variants. The original discoveries of virus variants multiplied the challenge of defining the public health significance of bat rabies, but at the same time, they helped clarify it. Nonetheless, the challenge continues to grow by disclosures of rare-to-frequent transmission of variants from one host species to another, sometimes with serial transmission thereafter, as described below in the section on intraspecies and interspecies transmission. Such host interspecies transfer of virus raises the specter of potentially unwelcome consequences, such as a change from a predominantly paralytic disease to unabated furious disease and consequent attacks.

Intraspecies and Interspecies Transmission of Bat Lyssaviral Variants

Lyssaviral variants can be transmitted between bats of the same species (intraspecies) or among bats of different species (interspecies). Intraspecies transmission seems evident when infection with like variants is present in both mother and suckling bats in the absence of contact with other sources of virus. Such conditions usually prevail in multimillion aggregations of Brazilian free-tailed bats. Similarly, the northern yellow bat, a solitary species that takes shelter in tree foliage, has been found rabies infected with its litter of three rabies-infected suckling offspring (Schneider and others, 1957). Also a lactating eastern red bat and her litter of four were all rabies infected (Birney and Rising, 1967). Newborn bats might be infected by their mother as she severs the **umbilical cord**, by licking infective saliva onto mucosal surfaces, by bites, or by aerosol in some environments. Conspecific mature bats probably are infected by various similar methods as they crowd together in shelters or interact at feeding or drinking sites. However, more than one colonial species sometimes live in the same shelter, where single or multiple interlopers may crowd into another species' cluster (Figs. 14 and 15), possibly to maintain body heat, whereupon bites might be exchanged. Thus, interspecies transmission of virus seems a logical source of virus variant differentiation within the recipient species over time (Box 7).

Although lyssaviruses usually are transmitted by bite, alternate exposure routes include aerosols, ingestion, and by contamination of wounds or mucosal surfaces with infective saliva or tissues (Johnson, 1965; Constantine, 1988a). These viruses may survive through additional possible and probable transmission routes, including insects. Although Mokola lyssavirus has been shown to replicate in inoculated mosquitoes, **biological transmission** by arthropods of that or other lyssaviruses has not yet been demonstrated.

Mechanical transmission by arthropods however, seems likely in certain situations. Dermestid beetles and their larvae, for example, consume the tissues of live or dead rabid bats in huge cave colonies of Brazilian free-tailed bats (Fig. 16), and the author has demonstrated rabies virus on the exteriors of both life stages of beetles recovered from the skull cavities of bats (Constantine, unpub. data). Adult beetles and larvae seeking flesh to eat will attack living or dead mammals, including humans. In so doing, the contaminated insects may be able to mechanically transmit the virus. The abdominal contents of beetles that feed on bats are known to be consumed by assassin bugs, which routinely attack mammals, including humans, for blood meals. Such rabies-contaminated bugs may also be able to mechanically transmit virus in this manner. Various **mites**, hordes of which parasitize bats, include species that consume fluids available at the edges of mouths, eyes, or within the nostrils or ears of bats as well as of human visitors to bat caves. Thus, these feeding habits may provide opportunities for interspecies mechanical transmission of virus.

Figure 14. A mixed group of pallid (light-colored) and Brazilian free-tailed (blue-grey) bats in an attic. (D.G. Constantine)

Figure 15. A Brazilian free-tailed bat (blue-grey) and a Yuma myotis bat (brown) cooperating to conserve body heat. (D.G. Constantine)

Figure 16. A dead Brazilian free-tailed bat being consumed by dermestid beetles commonly found in association with bat colonies. (D.G. Constantine)

Figure 17. Brazilian free-tailed bat. (D.G. Constantine)

Table 8. Examples of vampire bat rabies variants found in other species in Latin America.

Country	Date	Findings
Brazil	1998–2001	22 of 23 dog and cat rabies cases tested (Kotait and others, 2001).
	2000	32 of 53 non-vampire bat rabies cases tested, representing 16 different bat species (Silva, 2001).
	2001	A cat previously in contact with a bat developed rabies and infected its owner (Kotait and others, 2001).
Costa Rica	2001	An aggressive household cat bit two people who died of rabies of vampire bat origin (Badilla and others, 2003).
Mexico	1999–2001	Fruit bat and dog (Vargas Pino, 2001; Velasco Villa and others, 2001).
	2004	Child bitten by cat (Tesora Cruz and others, 2006).

The development of methods to recognize and classify viral variants by their host species of origin has helped to retrospectively identify the infection source, such as a particular species of bat or carnivore, putatively responsible for infecting a human victim (Rupprecht and others, 1991; Smith, 1989). Recent reports based on these techniques also indicate that a large amount of interspecies lyssavirus transmission has occurred between mammal species, especially from vampire bats to other bats and carnivores.

Latin America

Vampire bat rabies virus has been isolated from other bats and from carnivores in Latin America (Table 8). These findings indicate direct transmission of rabies by vampire bats or by other bats that might be serially transmitting the vampire rabies variant. Moreover, where Brazilian rabies vaccination campaigns had brought urban canine and feline rabies under control, the finding of a vampire rabies variant instead of a canine rabies variant as the cause of recent rabies cases in dogs and cats (Table 8) indicates that the vampire bat variant is transmitted serially among pets.

Reports of interspecies transmission of rabies by bats other than vampires refer nearly exclusively to insectivorous species. In Chile, where five rabies virus variants were studied, the Brazilian free-tailed bat (Fig. 17) was considered to be the source of a variant found in one human, dogs, cats, cows, and a pig. A variant typical of Western red bats or other members of the genus *Lasiurus* was recovered from a red bat, three Brazilian free-tailed bats, and a dog. It was suspected that livestock were infected by dogs or cats that had acquired the infection by attacking grounded bats, but none of the identified variants closely resembled variants associated with vampire bats (De Mattos, C.A. and others, 2001; Favi and others, 2002).

North America

There have been 51 known or presumed bat-transmitted human rabies infections in the USA (Messenger and others, 2002; Krebs and others, 2003; Krebs and others, 2004; Blanton and others, 2006) and Canada (Dempster and others, 1972; Varughese, 1983; Webster and others, 1987; Krebs and others, 2001; Krebs and others, 2004) from 1951 to 2006. Human cases were attributed to bat species based on bat carcass identification or prior association of rabies variants with a given bat species (Table 4). Bat carcasses were often unavailable for species identification and for comparison with identified virus variants. In cases where bat carcasses were available, tricolored bat virus variants were identified from a big brown bat, indicating interspecies transmission, and from a bat retrospectively identified by an untrained observer as an eastern red bat (Hardman and others, 1995). However, red bats and tricolored bats have similar pigment distribution in their wing membranes and could be confused with one another. In studies of rabies in Alaskan bats (Blanton and others, 2007), a little brown myotis was infected with a rabies variant associated with silver-haired bats, and a Keen's myotis was infected with a variant associated with eastern red bats. The frequent absence of a bat contact in the human victim's history also leaves open the possibility that an intermediate host, such as a cat that had chewed a rabid bat, might be the source of some human infections.

Transmission of rabies from bats to individual wild or domestic carnivores and livestock in the USA was implied in various earlier reports based on virus variant characteristics (Rupprecht and others, 1991). Notwithstanding the possibility of viral transmission by intermediate hosts, 28 animals (11 foxes, 1 skunk, 7 cats, 2 cows, 6 horses, and 1 sheep) were suspected of having been infected by 12 big brown bats, 8 eastern red bats, 2 Brazilian free-tailed bats, and 6 bats of undetermined species (Baer and Smith, 1991). A survey in Colorado designated a rabies variant identified from big brown bats as the infective agent in three skunks and one fox (De Mattos, C.C. and others, 2001). A study of rabies virus variants obtained from 19 skunks during a skunk rabies outbreak in Arizona indicated that those variants were nearly identical to a virus variant commonly found in big brown bats, the suspected source of the outbreak (Leslie and others, 2006). These results provide possible evidence of serial trans-

Box 7 Bat Versus Bat—Interspecies Transmission of Bat Lyssaviruses

In 1957, before rabies virus variants were known to exist, the author sought bat shelters in Mexico that were occupied by common vampire bats and migratory Brazilian free-tailed bats from the USA. The purpose of that inquiry was to explore the possibility that vampire bats might occasionally attack and drink the blood of insectivorous bats, as had been observed among captive bats. Such behavior would facilitate virus transmission from infected vampire bats. Alternatively, vampires might be infected by saliva-contaminated air in some free-tailed bat cave shelters or by retaliatory bites, and may be infected by free-tailed bat lyssavirus variants.

Brazilian free-tailed bat bitten and bled to death in captivity by a common vampire bat cage mate. (D.G. Constantine)

Several caves were found to be occupied by the two bat species. About 200,000 of the migratory free-tailed bats were in a large but shallow cave that also harbored 15 common vampire bats in a deep side tunnel. The free-tailed bats had little protection from weather, which if cold would render them lethargic and helpless, and if wet and stormy would discourage their evening departure and the departure of the vampires. Either condition would make the free-tailed bats readily available to the vampires, which die if they do not feed for 3 nights (McNab, 1973). Lyssavirus variants from the two species were later determined to be closely related (Franka and others, 2006). Other workers also found that captive vampire bats readily fed on insectivorous as well as frugivorous bat cagemates, and a frugivorous little yellow-shouldered bat in South America had a similar bite wound when it was captured in a cave shared with vampire bats (Lord and others, 1973).

mission of rabies among North American carnivores following acquisition of virus from bats. In addition, these outbreaks contrast with earlier single isolated occurrences of evident bat rabies variant transmission to carnivores in areas otherwise free of rabies in carnivores (Smith and others, 2001).

Europe

Few interspecies transmissions of lyssaviruses from bats have been reported in Europe, however fewer investigations have been done in Europe than in other regions. The five European human deaths of European bat lyssavirus (EBL) origin (Table 5) were mentioned earlier: one from EBL-2 in Scotland (Fooks and others, 2002; Fooks and others, 2003), one from EBL-1 in Russia (Selimov and others, 1989), one from EBL-2 in Finland (Lumio and others, 1986), and two from uncharacterized lyssaviruses in the Ukraine (Selimov and others, 1989; Botvinkin and others, 2005). In addition, three domestic sheep were reported infected with EBL-1 in Denmark (Stougaard and Ammendrup, 1998a; Stougaard and Ammendrup, 1998b), and a stone marten was infected with the same virus in Germany (Müller and others, 2001). It seems improbable that insectivorous bats would attack sheep, and it is possible that the virus was transmitted by a carnivore, such as a fox or cat that was infected as it attacked a grounded bat. The EBL-1 variant also was isolated from nonnative Egyptian fruit bats in zoos that had previously exchanged animals with Denmark, the Netherlands, and Belgium (Ronsholt and others, 1998). Presumably the infection originated from a native bat. The EBL-1 virus is most often associated with the serotine bat, although it is known from at least three other bat species in Europe (Appendix D).

The EBL-2 virus is known from two bat species, the pond bat in Denmark and the Netherlands and Daubenton's bat in Germany, Denmark, Switzerland, and England and Scotland in the United Kingdom. Transmissions of lyssaviruses from bats to other mammals seem to be rare in Europe, where most infected bats have been found in areas apparently free of infection in other species, comparable to many areas of North America.

Africa

Four lyssavirus species are currently known from mammals in Africa: classical rabies, Duvenhage bat, Lagos bat, and Mokola. Each of the four is divisible into variants, and the existence of multiple hosts for each virus species suggests previous interspecies transmission. Classical rabies is present in humans and in domestic and wild mammals, but it has not been identified in bats outside of the Americas. Only Duvenhage and Lagos bat lyssaviruses are currently known in **African bats**. In 1970, 2006, and 2007 Duvenhage bat virus caused the rabies-like deaths of two men in South Africa (Meredith and others, 1971; Paweska and others, 2006), and of a woman in Kenya (van Thiel and others, 2008). Each of these people were bitten or scratched by unidentified bats, although the bat in one case was said to have resembled the insectivorous long-fingered bat. Duvenhage bat virus has since then been recovered in South Africa from another bat resembling that species (Paweska and others, 2006) and in Zimbabwe from the insectivorous Egyptian slit-faced bat (Foggin, 1988). Additionally, an incompletely characterized lyssavirus was found in an unidentified bat in Zambia (Ahmadu and Zulu, 1998).

Lagos bat virus is known in straw-colored fruit bats in Nigeria and Senegal, Peters' lesser epauletted fruit bat in the Central African Republic, Wahlberg's epauletted fruit bat in South Africa, and in the insectivorous Gambian slit-faced bat in Senegal. In addition, it was reported in a domestic dog in Ethiopia, two domestic cats in South Africa and Zimbabwe, and a water mongoose in South Africa (Markotter and others, 2006a; Markotter and others, 2006b). Experimental infections of Lagos bat virus were demonstrated in dogs and rhesus monkeys (Percy and others, 1973). No human infections are known, but during a Lagos bat virus outbreak among fruit bats in South Africa, a motorcyclist was pursued and bitten on his face by a bat, which escaped. The bite victim received antirabies prophylaxis and did not develop clinical disease.

Mokola lyssavirus has not been confirmed in bats. Two human cases were identified in Nigeria; one of the victims survived (Familusi and others, 1972). The virus has also been isolated from an insectivorous rusty-bellied brush-furred rat in the Central African Republic (Saluzzo and others, 1984), a domestic cat in Ethiopia (Mebatsion and others, 1992), and domestic dogs and cats in Zimbabwe and South Africa (Foggin, 1982; Foggin, 1985; Sabeta and others, 2007). Mokola was also found in insectivorous Crocidura shrews in Nigeria and Cameroon. An association between shrews and bats is evident from observation of a Crocidura shrew feeding on an Angolian free-tailed bat within an attic colony (Osborne and Osborne, 1981). Experimental infections were demonstrated in **genets**, a mongoose, a jackal, dogs, and rhesus monkeys (Foggin, 1985; Percy and others, 1973).

Asia

Human lyssavirus infections from uncharacterized lyssavirus species were reported in two people previously bitten by bats; one infection was in a person in India who handled a disabled bat (Veeraraghavan, 1955) and the other was in a person in China, where a survey later disclosed infections in 3 of 300 unidentified bats (Tang and others, 2005). Similar infections were reported in the greater horseshoe bat in Turkey, the northern bat and Daubenton's bat in the Asiatic part of the Russian Federation, and the Indian flying fox in India. Aravan lyssavirus was discovered in the lesser mouse-eared bat in Kyrghystan (Arai and others, 2003; Botvinkin and others, 2003), and Khujand bat lyssavirus was recovered from the whiskered bat in eastern Siberia. However, a 1967 report of rabies infection in two bats in Thailand (Smith and others, 1967) was later reported to the author by the laboratory of origin to have likely resulted from laboratory contamination rather than originating from the bats in question.

A survey of healthy bats in the Philippine Islands failed to yield lyssaviruses from 821 insectivorous or **frugivorous** bats, which is similar to the results from earlier surveys of clinically normal bats globally, but 9.5 percent of 231 bats had antibodies against Australian bat lyssavirus (Arguin and others, 2002). Similarly, no lyssaviruses were recovered from 212 healthy bats in Bangladesh, but 3 of 127 Indian fruit bats had antibodies against the bat lyssaviruses Aravan and Khujand (Kuzmin and others, 2006). Sampling of bats in Thailand indicated that 15 of 335 Lyle's flying fox fruit bats and 1 of 45 lesser dawn fruit bats had antibodies against Aravan, Khujand, Irkut, or Australian bat lyssaviruses (Lumbertdacha and others, 2005). The survey results were interpreted as evidence of the presence of lyssaviruses but of a low prevalence of infection.

Australia

Australia was considered free of lyssaviruses until 1995, when a new lyssavirus species (genotype 7), now known as Australian bat lyssavirus, was first observed to produce signs of aggression and, ultimately paralysis and death in black flying foxes (Fraser and others, 1996). Some infected bats repeatedly and severely attacked and bit others of the species, including the offspring of one attacker. By 1999, surveys found the virus in 42 flying foxes, including members of 3 additional species: the little red flying fox, the gray-headed flying fox, and the spectacled flying fox. In addition, an Australian bat lyssavirus variant was found in four yellow-bellied sheathtail bats (Warrilow and others, 2003). Two female bat caregivers are now known to have died of the disease, one from the sheathtail bat variant and the other from a flying fox variant (Mackenzie, 1999). As mentioned above, antibodies against Australian bat lyssavirus were detected in bats in the Philippine Islands and in Thailand, indicating distribution of the virus well beyond Australia (Arguin and others, 2002; Lumbertdacha and others, 2005). The existence of multiple variants of this virus in various host species suggests past, if not continuing interspecies transmission, the latter demonstrated by the human cases.

Environmental Persistence

Rabies mortality in bats usually goes unnoticed because many bats die in their shelters, while others fall with folded wings into dense vegetation. Even multiple mortalities may hardly be noticeable for similar reasons. In some ways, bat mortality from rabies is comparable to a grass fire. The virus is represented by a burning match and the host mammal population by a field of dry grass. If a lit match drops where the grass is dense, a substantial and noticeable fire results, destroying nearly all of the grass. In time the grass regrows and the process may be repeated. However, if the grass blades are widely separated, only one or a few blades may burn unnoticed – the density of the grass being the key factor. Similarly, if a bat population is dense, it supports rabies transmission between individuals more readily, and thus the population is reduced (Constantine, unpub. data). Rabies infections may not be obvious in less dense populations.

Cyclic fluctuations and environmental persistence of bat populations and lyssaviral infections are influenced by several main factors (Fig. 18). A favorable climate is required to produce the plant base of the bat food supply: insects for insectivorous bats, fruit for frugivorous bats, and cattle as the blood source for vampire bats. Additional factors, differing by bat species, include such things as antibody systems and the amount of antibodies in the body, solitary or colonial habits, hibernation or migration habits, the numbers of young or litters produced per year, and alternate virus transmission routes. In addition, prolonged incubation periods provide a mechanism for virus persistence during the winter (Box 8). The overall effect of natural lyssavirus-caused mortality in bats may contribute to keeping host populations and food resources in balance without doing irreversible harm to either. This "balancing act" works despite some ghastly aspects of the scenario.

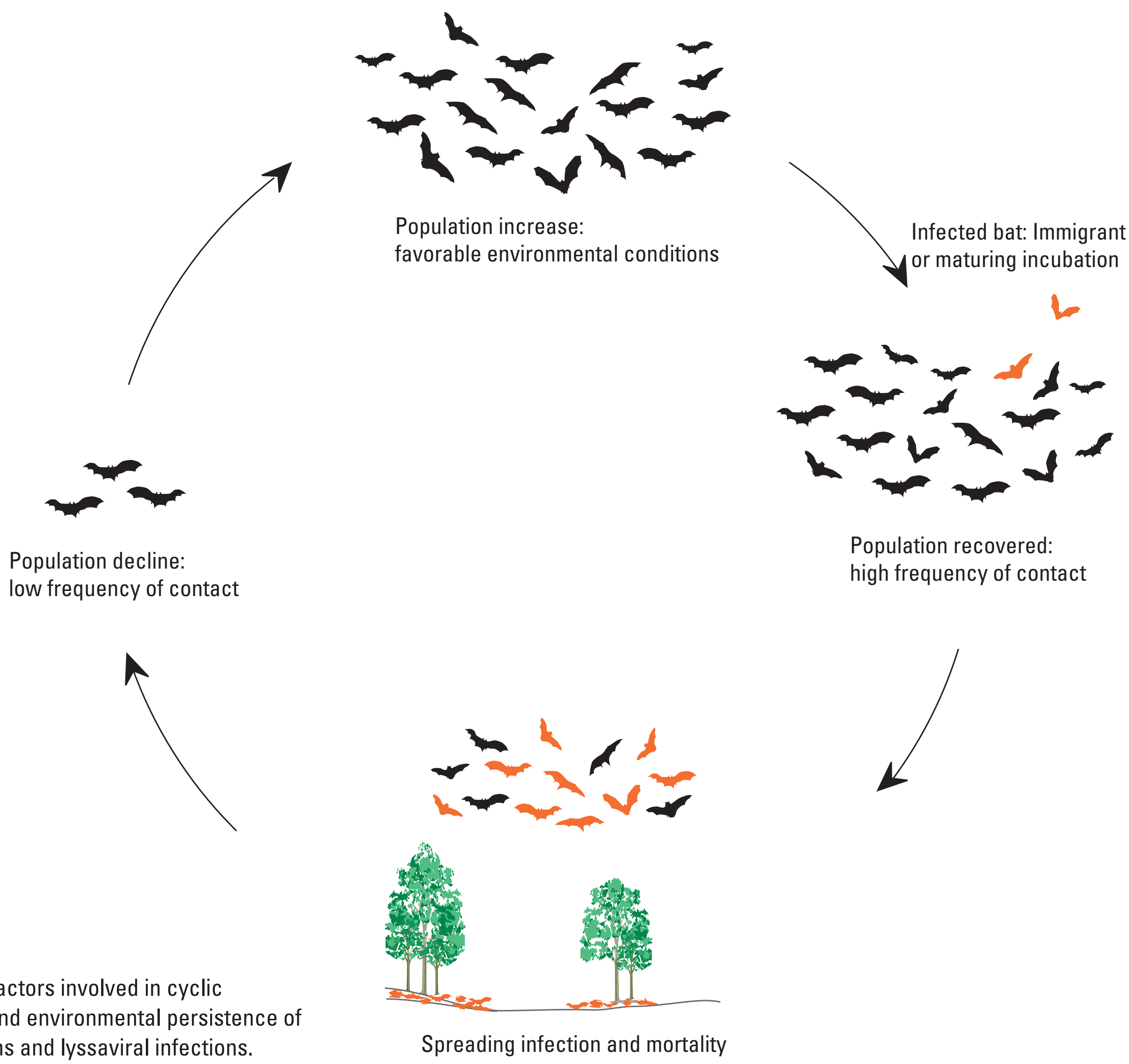
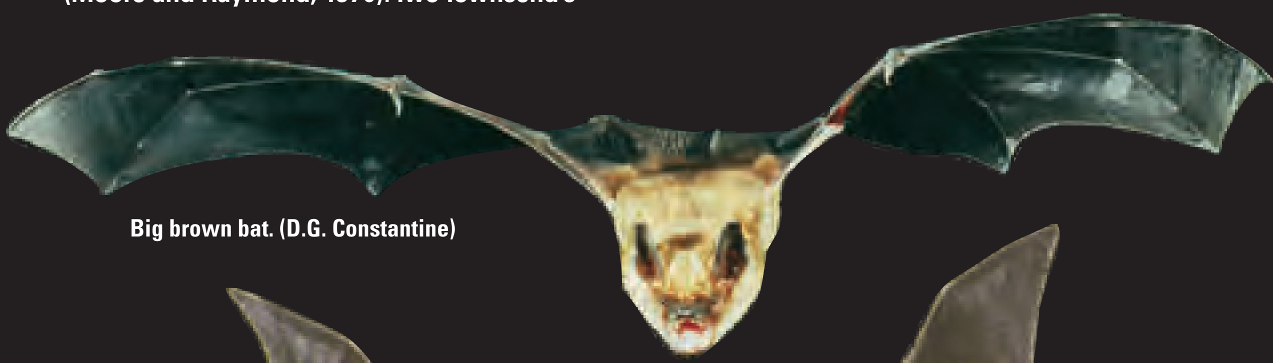


Figure 18. Factors involved in cyclic fluctuations and environmental persistence of bat populations and lyssaviral infections.

Lyssaviruses—Deadly Hitchhikers

Box 8

Long incubation periods, in some cases extended by hibernation, enable rabies virus and other lyssaviruses to survive within seemingly healthy bats for more than 7 months before the appearance of clinical signs of disease. During this period of apparent dormancy, a migratory bat may transport a virus along both legs of its journey of as many as 4,000 kilometers. For example, a big brown bat that was captured in North America before winter hibernation, and kept active and isolated all winter while fed in captivity, developed rabies 7 months later or 1 month after it would have awakened from hibernation (Moore and Raymond, 1970). Two Townsend's big-eared bats of North America, awakened from hibernation in mine tunnels in New Mexico and adapted to captivity in a warm environment, developed the disease nearly 3 months later, or about 7 months after they entered hibernation (Constantine, 1967a). Brazilian free-tailed bats that were caught in New Mexico and similarly held captive after they otherwise would have migrated southward died of rabies after periods of 7 days to 3 months (Constantine, 1967a). These examples illustrate methods by which bat rabies virus persists overwinter in the apparent or actual absence of bats.



Big brown bat. (D.G. Constantine)

Townsend's big-eared bat hovering over water with tongue extended to drink.
(D.G. Constantine)

Points to Ponder: Interspecies Interactions in Potential Bat Rabies Transmission Settings

Intertwined with lyssavirus disease ecology are the interspecies interactions that develop when humans, their domestic animals, or other animals invade or otherwise interact in a setting where the potential for disease transmission exists. Cats play an especially important role in bat lyssavirus exposures (see Box 9 and Disease Prevention and Control).

Bat Colonies in Manmade Structures

Insectivorous bats have long provided services to mankind by controlling insects that attack and spread diseases to humans, livestock, crops, and forests (Constantine, 1970). Furthermore, vegetarian bats, as the sole pollinators and seed distributors of many major tropical food plants (Constantine, 1970), have and continue to make possible human and other life in tropical areas. Fear of bat rabies, however, has often resulted in the persecution of bats associated with manmade structures, and this fear has generally been fed by a lack of understanding of the ecology of bats.

Upon the discovery of bat rabies in the USA in 1953, frightening news stories repeatedly appeared, alarming homeowners and others whose buildings sheltered bats. Not knowing what to do but agreeing with public demands that killing the bats seemed appropriate, government agencies readily obliged by turning their mosquito control DDT foggers against bats and encouraged others to do likewise. Other toxicants were used after DDT was banned (Tuttle, 1988). This reaction resulted in widespread grounding of poisoned bats, which resembled rabid bats. An approximately tenfold increase in bitten people and pets followed, and most people received antirabies treatment and pets either were destroyed or quarantined after biting bats were discarded or escaped. A cycle of near-hysteria developed as poisons in typically unclosed bat harborages continued to act, sickening replacement bats for many years, leading to further poison applications and more frightening news coverage. Finally, efforts by those who understood these events prevailed over panic and politics, and toxicant use fell into disrepute (Tuttle, 1988).

Bats usually take shelter in elevated sites from which they can easily take flight (Figs. 19 and 20). They are noticeable due to their squeaking vocalizations, departures and arrivals, accumulations of droppings under their entry sites, or odors. Bats ill with lyssavirus infections may occasionally fall from these colonies (Fig. 21), whereupon predators such as cats, or curious people, are attracted to them resulting in bites and disease exposures. Whereas uninformed or fearful people often assume that destruction of bat colonies is the evident solution, that act is counterproductive, and a compromise such as excluding rather than killing the bats may benefit both bats and humans.

The exclusion of bat colonies and the sealing of bat shelters to prevent reentry are sometimes appropriate, especially when large colonies are located in school buildings where children may pick up fallen bats and be bitten. In another example, hundreds of bats were lodged in slots under an urban concrete bridge, from which boys pried dozens of young, flightless bats and threw them through the open windows of passing automobiles (Constantine, unpub. data). Ordinarily, exclusion of bats should not be undertaken until all of the young bats can fly and join mature bats on nightly foraging flights, which usually occurs by late summer or early fall. Otherwise, the young bats will be sealed inside the shelter to die and decompose, or they may crawl into building interiors where human and pet contacts may result. Exclusion is achieved by sealing all but the main exit and entry passages and arranging simple one-way valve-like systems over the exits, permitting bats to leave but preventing re-entry (Fig. 22) (Constantine, 1982b; Frantz, 1986).

Figure 19. An evening foraging flight of Brazilian free-tailed bats. (D.G. Constantine)

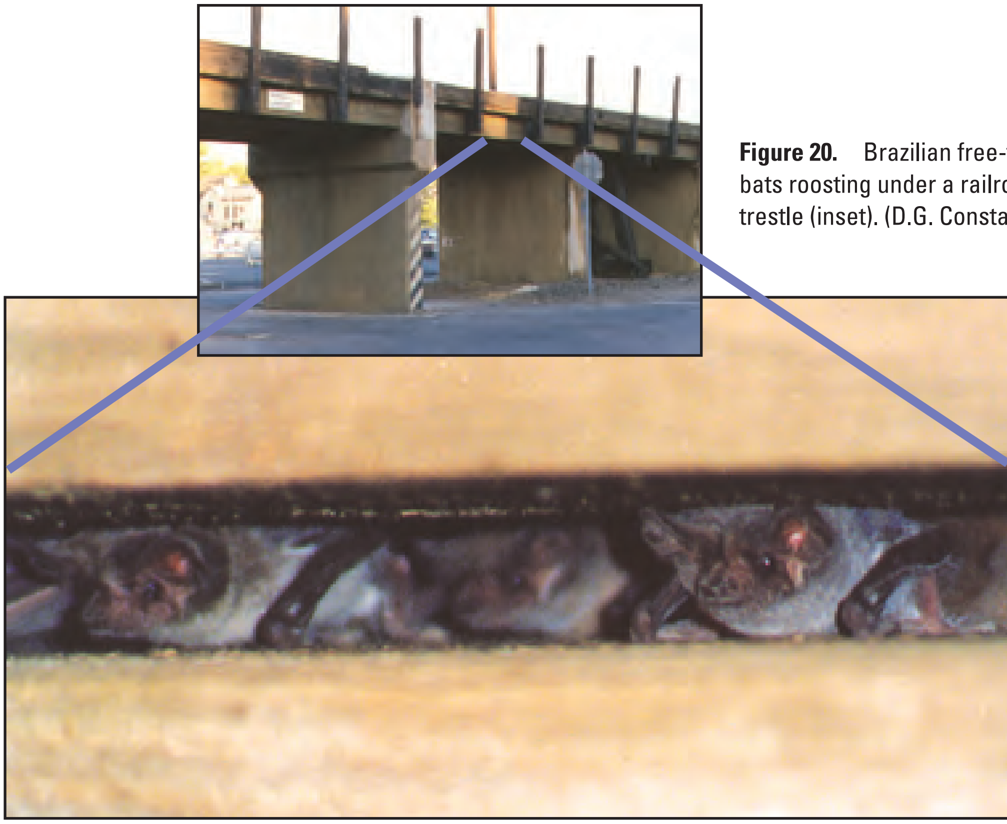


Figure 20. Brazilian free-tailed bats roosting under a railroad trestle (inset). (D.G. Constantine)

Figure 21. A dead Brazilian free-tailed bat lying on the guano-covered floor of a bat cave. (D.G. Constantine)

Box 9 Domestic Cats and Lyssavirus Transmission

(Photo by M. Friend)

It was easy to comprehend the extreme concern of a panicked mother who found her baby mouthing a bat delivered by the family cat (Constantine, unpub. data). In areas of the world where domestic cats are popular as pets or for rodent control, they are the primary predators of bats. The irrepressible hunting habits of domestic cats—and their practice of bringing home their victims—accounts for the great majority of contacts between people and bats. In the USA, approximately 10 percent of bats that are home-delivered by domestic cats prove to be infected with lyssavirus.

Cats readily jump fences to forage widely, whereas dogs are restricted to yards or tethered where they may be left with a bat courtesy of the family cat. Reports from 1 California county over a 14-year period revealed that 1 or more resident cats were found with 428 (66 percent) of the 649 seemingly ill, injured, or dead bats that appeared at residences. Dogs and cats were present together with 26 of the bats (4 percent), but only dogs were found with 52 of the bats (8 percent), an unknown number of which may have been delivered by resident cats (Constantine, unpub. data).

As mentioned elsewhere, most individual temperate zone bats become inactive when they are resting, are ill or injured, or as a consequence of cool ambient temperatures. These bats may appear to be dead and are easy prey for cats. A cat sometimes enters a residence with an unnoticed bat in its mouth, and having delivered its catch, the cat usually loses interest in the seemingly lifeless bat and leaves it on the floor. Later, as the bat warms, it seeks a vertical surface where it can climb to safety or a site from which it can launch itself into flight. Alternatively, especially if the bat is ill, it may remain hidden during daytime and initiate its upward climb after dark. The bat may climb blankets onto a bed or be chilled by the night air and seek a warm place, possibly next to the body of a sleeping human. As the person turns during the night and makes contact with the bat, it may inflict a retaliatory bite that might not awaken the sleeper. This scenario has occurred many times, involving infected as well as uninfected bats, and human rabies mortality likely has resulted. Six such rabies exposures are recorded in California (Constantine, unpub. data).

A Lyle's flying fox in Thailand climbs from the ground and up a tree trunk to reach the colonial roosting site, demonstrating the climbing behavior of bats. (D.G. Constantine)

Cats generally bite and chew to stun, kill, or eat a bat, and if the bat is infected then the interior of the cat's mouth can become contaminated with virus. Two relevant hazards can result: (1) the contaminated mouth of the cat may temporarily have the ability to mechanically transmit the virus by bite, by licking the virus into even slight wounds or onto mucosal surfaces, or by scratches with claws (Tabel and others, 1974) that were licked previously during cleaning or preening; (2) the cat may ultimately develop the disease, especially if it was not previously vaccinated, often vanishing to die in hiding as overt signs appear. Twenty-six likely human rabies exposures in California resulted from people being bitten by cats while they were trying to extract rabid bats held between the cat's teeth (Constantine, unpub. data). The possibility also exists for virus transmission through aerosolized oral or nasal fluids expelled as a cat sneezes, which is a demonstrated route of transmission for plague (Gage and others, 2000). Variations of such disease exposures could follow unobserved encounters between cats and infected bats and may account for many of the unexplained human lyssavirus deaths involving virus variants characteristic of bats but lacking histories involving bats.

Through variations of the scenarios described above, domestic cats are likely intermediate rabies hosts or vectors between bats and humans. Cats are relatively resistant to rabies; a cat exposed to rabies may never develop the disease and thus be above suspicion. In laboratory experiments, striped skunks could be infected by eating the carcass of a single mouse infected with rabies virus of silver-haired bat origin, but cats fed 25 such carcasses were not infected (Bell and Moore, 1971). Moreover, a cat may eat an infected bat and return home with a contaminated mouth and claws. Alternately, a cat may eat a rabid bat after it has bitten a person, thus precluding the bat from being tested and consequently discouraging the human bite victim from seeking treatment. This happened in Wisconsin in 1959, and it resulted in a documented human rabies mortality (Humphrey and others, 1960).

(Photos by M. Friend)

Rabies in cats is a "spill-over" or incidental infection transmitted to a cat by a reservoir host: a rabid dog, wild carnivore, or bat. In the USA, annual reports of rabid cats ranged from 200 to 500 cases per year between 1938 and 1960 (Rupprecht and Childs, 1996). During this same time period, however, dog rabies cases typically outnumbered cat cases by a factor of 10 or more (Rupprecht and Childs, 1996). Canine rabies vaccination campaigns initiated in the 1950s led to a drastic reduction in dog cases, but at the time, far less emphasis was placed on cat rabies vaccination. Thus by 1981, as dog rabies came under control, cat rabies cases increased so that they exceeded dog cases and they have maintained their lead since.

This trend may be explained by the popularity of cats as pets, by their relative risk of encountering rabid animals when allowed to roam freely, and by difficulties in the enforcement of mandated cat rabies vaccination (Rupprecht and Childs, 1996). In addition, since the discovery of bat rabies in the USA in the early 1950s and the consequent alarm when cats bring home rabid bats, increasing numbers of cats have been sacrificed and tested for rabies. The relative rabies resistance of cats, coupled with the lower rabies dose received from a typical bat bite, probably results in fewer cat rabies infections from bats than from bites that roaming cats may receive from rabid skunks, foxes, or raccoons. However, this does not diminish the danger to people from mechanical or biological transmission of rabies by pet cats.

The obvious solution to this problem is to keep domestic cats confined indoors and to ensure that they are up-to-date on vaccinations. Hunting cats bring home an amazing variety of diseases and disease-transmitting parasites that they either carry themselves or have acquired from wildlife. Some diseases acquired this way by humans, such as plague (Gage and others, 2000; Baldwin and others, 1991), are treatable if they are recognized early enough, but only three or four people are known to have survived lyssavirus infections. Stray cats and feral cats may also transmit diseases and parasites---including some feline diseases that neutralize the protective effects of vaccinations---to owned cats (Pedersen and others, 1985; Yamamoto and others, 1989). The prompt testing of bats that are found under circumstances resembling any of the foregoing scenarios may reveal lyssavirus infection, and thus initiate prophylaxis specific to the found variant to potentially infected humans. Management of pets as directed under Disease Prevention and Control would decrease disease transmission to other pets, wildlife, and people.

Figure 22. Exclusion devices permit bats to depart from but prevent re-entering the interior of a building. Bats enter and exit buildings through very narrow openings that may be revealed by soiled areas such as ***A***, attic vent louvers, or ***B***, fascia. Buildings can be bat-proofed by installation of simple valve-like devices such as ***C*** and ***D*** that allow bats to exit but prevent entry (Constantine, 1982b).

Bat Colonies in Caves and Mine Tunnels

Most caves or mine tunnels in North America are devoid of bats. Some, however, may be inhabited only in summer, others only in winter, and still others year-round. If bats are present, their numbers usually vary from 1 to 30, but sometimes to several hundred or more. Some bat species hide in crevices, but others are more exposed and obvious. Summer shelters are warm to hot, and bats may be active. Winter shelters of most species are cold, facilitating the hibernation of bats, individually or in compact groups.

Some bats do not survive human intrusions due to injuries or predation outside or inside the shelter, and human intrusion may cause bats to abandon shelters. Hibernating bats often slowly awaken and move to safer places after someone tries to noiselessly sneak past them, which can sometimes result in the loss of sufficient body fat for the bat to survive until spring. When a person enters in summer, pandemonium can result as bats panic to avoid intruders. Some bats may fly outside while others retreat to deeper sites to escape the intruder. Flightless suckling bats often become dislodged and fall or are panicked into clumsy attempts at flight. Such young bats or distressed adults may fall or land on human intruders, who may be scratched or even bitten, especially if they slap or grab the bat. Thus, the intruder has experienced a potential lyssavirus exposure. Human avoidance of bat shelters benefits bats by removing the potential for disrupted hibernation, and benefits people by removing the potential for disease transmission from bats.

Figure 23. Researcher among a Brazilian free-tailed bat colony. Note the personal protective clothing and equipment worn, such as coveralls, gloves, respirator, and hat; eye protection is also recommended. (D.G. Constantine)

The danger of rabies transmission by inhalation of airborne virus is known to exist in caves occupied by many thousands to millions of Brazilian free-tailed bats (Fig. 23) (Constantine, 1967b; see also “Cave Explorations” below). This danger becomes greater as bat numbers increase or as cave space decreases proportionately, and similar caves crowded with other bat species in tropical areas pose similar danger. Prohibition of the entry of humans into such shelters during seasons of bat occupancy, except for persons willing to risk exposure after they have received proved effective pre-exposure antirabies immunizations, decreases the risk of infection by aerosol or other means of transmission. Depending on location, such visitors may also be exposed to excessive heat, humidity, noxious cave gasses (such as ammonia), carnivorous beetles, blood-sucking and other **arthropods**, snakes, mammalian predators ranging from skunks to **jaguars**, and other hazards, including **histoplasmosis** (Constantine, 1988a). The latter tuberculosis-like fungal disease is acquired by inhaling infective spores in **guano** dust. Relevant warning signs have been erected at some caves in the USA.

Special gates that permit bat passage but that block human entry have been installed at the entrances of some bat caves and mine tunnels to protect the much smaller groups of bats that shelter therein. However, similar gates would probably kill many bats as they rapidly enter or depart en masse at multimillion-bat colonies.

Flying Bats that Enter Buildings at Night

A flying bat occasionally enters a residence through an open window or door at night, because it recognizes the light inside as an attractant for its flying insect food. In this situation, the bat is likely to depart the same way it entered if doors to other rooms are closed to prevent it from getting lost in adjacent rooms. If the bat clings near the ceiling, it can be encouraged to leave by intimidation with a broom, or it may be captured carefully in a butterfly net or by placing an open coffee can over it and sliding a cardboard lid behind the can opening to keep the bat inside. Capture technique may have to be varied or improvised if the bat falls to the floor or does not cooperate. Such a bat is unlikely to be infected, but there are no guarantees, and bites or scratches should be regarded as potential rabies exposures unless the bat is quickly tested and proved uninfected. In the absence of skin contact, the bat may be released outside. Window and door screens discourage such bat visits.

Alternatively, a bat may enter through an unscreened chimney, sometimes attracted by exiting warm air on cool evenings, or it may gain entry by unknown means. It may enter a darkened building at night seeking temporary rest, shelter from wind or rain, warmth, or perhaps a new home or stopover site while migrating, and it may be discovered the following morning. As with any mysterious appearance of a bat, one cannot know if the bat was delivered by a resident—and thus potentially exposed—pet cat. One would prefer to be assured that no humans or pets have been exposed to rabies, but that is impossible, especially if the bat has been in a bedroom with a sleeping person. The teeth of many bats are sharp but short and may be capable of transmitting virus without awakening bitten persons or leaving detectable bite wounds. Healthy adults evidently have not awakened to bites, and others, such as infants, elderly, or medicated persons may be unable to perceive or communicate events. At least 30 percent of 51 North American human rabies victims were either awakened at night during a rabid bat attack or the bat was present in their bedrooms when they awoke in the morning (Constantine, unpub. data). Also, sound can precipitate rabid bat attacks, and any source of sound in an otherwise quiet bedroom may be a target. Snoring or even faint noises such as air movement through partially closed lips may suffice to attract a rabid bat.

Unprovoked Attacks by Flying Rabid Bats

Attacks on people and noisy pets by flying rabid bats are rare in the USA. Most reports involve the canyon bat (Fig. 10), which is abundant in the Southwest and prefers to shelter in rock crevices in cliffs. Fewer attacks are documented for the Western small-footed myotis (Fig. 11) and the California myotis (Fig. 12), both of which prefer to shelter in rock crevices, under loose tree bark, or other similar natural sites. All three species are strictly solitary and uncommonly take shelter in buildings. Flying attacks by rabid bats of other common North American species have been documented. The flying attacks are known to be swift and direct, and the bat is not seen until it has bitten the victim. That said, it seems superfluous to mention the only potentially preventive measure: do not make noise or do anything that may attract the animal's attention. Most attacks have occurred in daylight, so bats flying in daytime should be suspect. Daylight attacks by rabid bats have been reported in Latin America (Haupt and Rehaag, 1921; Torres and de Quieroz Lima, 1935; Pawan, 1936), but few case-specific details are available.

Translocation of Bats

Bats have been and continue to be accidentally and intentionally translocated by intra- and intercontinental ships, aircraft, and overland transport. Some of these bats may be incubating infectious diseases such as lyssaviruses. Bats are intentionally translocated to stock zoos or laboratory colonies and to supplement wild populations. Some bats intended for translocation have escaped en route to or at their destinations (Constantine, 2003). Only a small fraction of translocations are publicized, and they typically are highlighted only after information is released following accidents. Among various objections to translocations, especially when bats escape, are the potential introduction of foreign diseases that could impact humans and animals. For example, the recent introduction of West Nile virus into North America may have been due to the importation of thousands of foreign fruit bats for sale as pets and for exhibition (Constantine, 2003). In addition, a live little free-tailed bat was inadvertently transported by aircraft in a suitcase from South Africa to Los Angeles. This species is one of the very few known to support the experimental replication of the **Ebola** virus without exhibiting clinical signs of the disease (Swanepoel and others, 1996). Increased regulation of the wildlife pet trade within the USA was urged following the accidental introduction of **monkeypox** virus, which was brought into the country by small African mammals intended for the pet market (Reynolds and others, 2007). The need for wildlife health certification for translocated and released wildlife has been elevated during recent years (Friend, 2006).

Vampire Bats and Rabies

Vampire bat populations, once dependent on native fauna for their blood meals, increased greatly following the introduction of domestic livestock throughout Latin America (Greenhall, 1988). Three different vampire bat species are involved in rabies transmission (Box 10). Rabies outbreaks in vampire bats (Fig. 24) have been observed to "migrate" throughout vampire populations, often along rivers, leaving a wake of death as the disease kills both the bats and livestock. Because vampire bats prefer feeding from cattle, the bats usually turn to other victims, including people, only after cattle die or are moved seasonally to distant pastures. Cattle depredations can be controlled by destroying vampire bat populations. This objective can be achieved through campaigns whereby petroleum jelly that contains an anticoagulant is applied to the backs of captured vampires (Fig. 25) that are then released to return home, where companion vampires lick off the jelly and perish as a consequence. Alternatively, the jelly is applied to wounds on bitten animals (Fig. 26) to poison vampire bats that return to the wounds on subsequent nights (Lord, 1988).

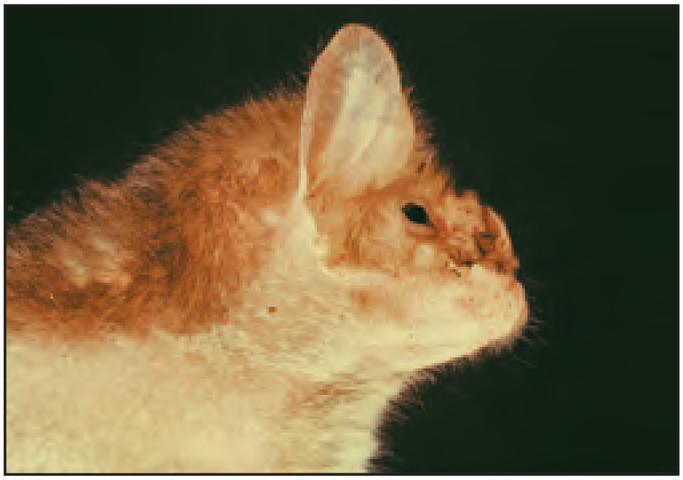


Figure 24. Common vampire bat. (D.G. Constantine)

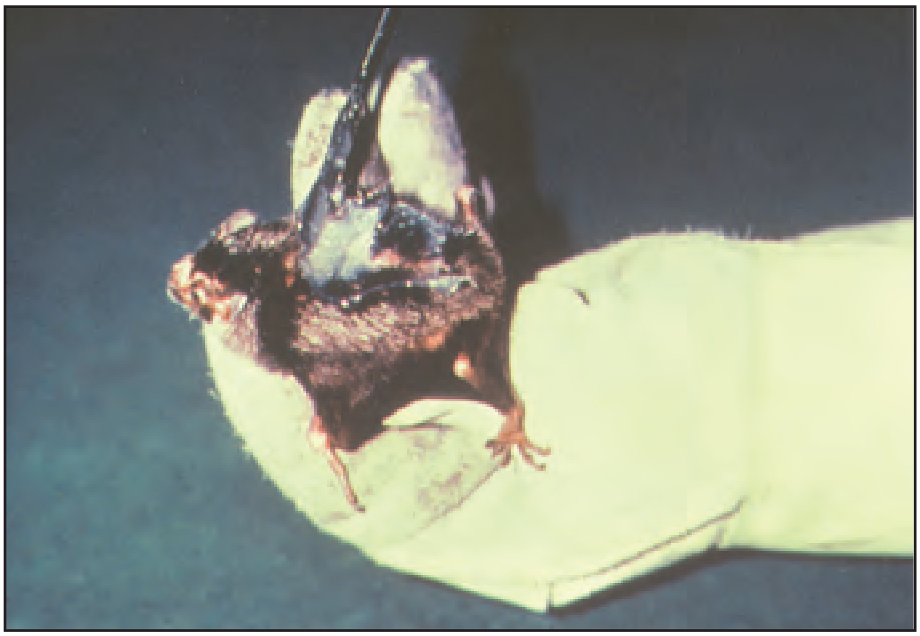


Figure 25. Application of anticoagulant jelly to the back of a vampire bat. (D.G. Constantine)

Figure 26. Vampire bat-bitten burro. (D.G. Constantine)

Box 10 The Tripartite Vampire Bat Clan

Although most references to vampire bats refer to the common vampire, two less abundant vampire bat species exist that prefer the blood of birds, including poultry. These species, the white-winged vampire and the hairy-legged vampire, bite birds on the legs or the cloaca region from the underside of branches on which the birds perch (Greenhall, 1988), but these bats will also feed on the blood of mammals, including humans.

All three vampire species are distributed from Mexico to southern Brazil or Argentina and exhibit unique characteristics and behaviors. The white-winged vampire bat has white wing tips and a large, bulbous gland within each of its cheeks, from which it can emit through its open mouth a jet of liquid similar to the anal scent gland secretion sprayed by skunks. In contrast, the hairy-legged vampire bat is solitary and retiring rather than gregarious and confrontational. The

Reported distribution of the three species of vampire bats: the common vampire bat (Greenhall and others, 1983), the hairy-legged vampire bat (Greenhall and others, 1984), and the white-winged vampire bat (Greenhall and Schutt, Jr., 1996).

EXPLANATION

- Reported range of the common vampire bat (*Desmodus rotundus*)
- Reported range of the hairy-legged vampire bat (*Diphylla ecaudata*)
- ★ One hairy-legged vampire bat was found in the USA
- ● Documented geographic locations of the white-winged vampire bat (*Diaemus youngi*)


Common vampire bat. (D.G. Constantine)

common vampire bat frequently regurgitates blood to supplement milk for its progeny older than 3 months of age. It also shares regurgitated blood with females that failed to secure meals through predation. Such food sharing among adult vampire bats is performed on a basis of reciprocity, requests from previously uncooperative bats being rejected.

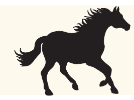
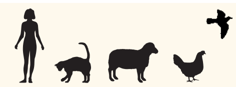
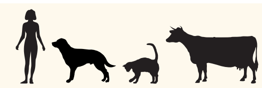
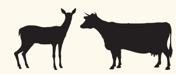
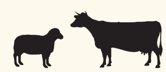
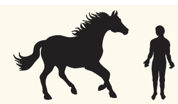

White-winged vampire bat. (D.G. Constantine)


Hairy-legged vampire bat. (D.G. Constantine)

Three species of vampire bats would be sufficient, but current research indicates that the common vampire may be divisible into additional species (Martins and others, 2007). In addition, the presumed extinct giant vampire bat may yet be found living (Ray and others, 1988).

Table 9. Diseases other than rabies that may be transmitted by vampire bats.

[The feeding habits of vampire bats provide a mechanism for mechanical transmission of infectious agents to their live animal food sources.]

Disease	Causative agent	Agent type	Primary hosts
Chagas disease	*Trypanosoma cruzi*	Protozoan	Humans 
Murrina (Surra)	*Trypanosoma evansi*	Protozoan	Horses 
Candidiasis	*Candida chiropterorum*, etc.	Fungus	Mammals, birds 
Salmonellosis	*Salmonella enterica* serotype Typhimurium, etc.	Bacterium	Mammals 
Brucellosis	*Brucella abortus*, *B. suis*, etc.	Bacterium	Cloven-hooved mammals 
Foot and mouth disease	Aphthovirus foot and mouth disease virus (FMDV)	Virus	Cloven-hooved mammals 
Venezuelan equine encephalomyelitis	Alphavirus Venezuelan encephalomyelitis virus (VEEV)	Virus	Horses, humans 

Attacks on People

Vampire bats may transmit numerous other known or potential diseases, in addition to rabies (Table 9) (Constantine, 1988b). Most vampire bat attacks on people are in undeveloped areas, where victims often do not recognize the cause of bites inflicted during sleep and darkness, or ascribe them to mythical agents such as witches, thus emphasizing the need for education. However, furious daytime attacks on people and animals have been reported during rabies outbreaks throughout Latin America (Pawan, 1936).

Physical exclusion of bats from the dwellings of remote native peoples most affected may be nearly impossible due to the primitive nature of these shelters and due to the lack of funding to construct more secure quarters. Infection would be preventable by pre-exposure antirabies vaccinations, which may be prohibitively expensive, or postexposure treatment with suitable vaccine and globulin products, which generally are neither affordable nor available. Under these circumstances, the potential for infection may be reduced by immediately and extensively washing the bite wound with soap and water, irrigating the wound with a virucidal agent, promptly testing the bat, and starting the patient on postexposure treatment. In view of the general unavailability of modern preventive measures, native peoples could benefit from revisiting the rabies-preventive measures that their predecessors taught the European explorers during the early 1500s: promptly cleanse vampire bat wounds and cauterize them with wood embers.

Attacks on Livestock

In addition to vampire bat population control methods mentioned above, vampire-borne rabies in livestock can be limited by various other methods, the most effective of which is antirabies vaccination of livestock. Recent studies have revealed the existence of at least three rabies virus variants that are circulating among vampire bats in Latin America, and each variant has a specific geographical distribution that may differ from or overlap with that of other variants (De Mattos, C.A. and others, 2001; Vargas Pino, 2001). Consequently, antirabies vaccines tailored to each or all of these variants might increase their effectiveness.

Attacks on Domestic Dogs and Cats

Vampire bats may expose companion dogs or cats to rabies while seeking blood meals or under other circumstances (Box 9). Cats in particular may collect and deliver live or dead vampires, some captured as they attack the cat. Vampire bats can deliver exceptionally effective bites, and thus greater virus doses. They usually remove a divot of flesh about 1/8 inch (3 millimeters) in diameter with each bite, and they will do so either defensively for protection or to obtain blood for feeding. Rabies of vampire bat origin has adapted to and is being transmitted serially among dogs, cats, and some other bat species in Latin America (Carrieri and others, 2001; Kotait and others 2001). Infected dogs or cats may then transmit rabies to humans or to other mammals. The prompt testing of a rabies-suspect vampire bat may indicate if it is infected. If the bat involved in an attack is unavailable or unsuitable for testing, or if testing is delayed, then the bat should be considered infected and known or potentially exposed subjects should be managed accordingly (see Disease Prevention and Control). This problem can be limited by vaccinating pets against rabies and confining them to prevent their contact with vampire bats. Control of stray and feral dogs and cats would mitigate their chance of infection and subsequent roles as virus sources.

Attacks on Other Bats

Vampire bats deliberately attack other mammals, including other bat species, for blood meals, and other bat species serially transmit vampire rabies variants (Lord and others, 1973; Silva, 2001; Table 8). It is unknown if such changing of hosts will affect the nature of disease in the new host, such as changing a predominantly paralytic disease to a predominantly furious disease. Reports of furious rabies in various species of bats in Latin America are increasing, but more definitive evidence would delineate, qualify, and quantify relevant facts pertinent to devising appropriate responses or solutions.

Disease Prevention and Control

Preemptive actions to minimize exposure to rabid bats are possible (Table 10), and they can be highly effective when they are combined with sensible behaviors, such as avoiding hazardous situations and seeking treatment following potential exposure. When someone is potentially exposed to disease after being bitten by a bat or another mammal, the wound should immediately be scrubbed with water and soap and preferably irrigated with a virucidal agent, such as povidone-iodine solution. The victim should simultaneously take steps to initiate subsequent antirabies treatment. In addition, prompt testing of the bat may provide information valuable to treatment of the victim. However, if the bat is lost among a group of bats, one must consider whether it is possible or legal to capture and test all of the bats or to undertake treatment without further delay. Procrastination in seeking treatment can have a deadly outcome. The following sections provide general guidance and describe special circumstances when basic actions would be likely to mitigate the risk of disease or the severity of the infection.

Humans

Information about human rabies prevention is available from the Recommendations of the Advisory Committee on Immunization Practices (Centers for Disease Control and Prevention, 2008), which reviews rabies biologics, pre-exposure vaccination, postexposure prophylaxis, serologic testing, adverse reactions, and precautions. Additionally, current information referable to all lyssavirus laboratory services or biologics may be sought from local to international health department channels. The World Health Organization (WHO), Geneva, Switzerland, has designated various laboratories as WHO Collaborating Centers for lyssavirus reference and research.

Persons who work with rabies virus or with known or potentially infected animals can reduce their risk of infection by avoiding bites or other exposures and by receiving pre-exposure vaccinations followed by periodic tests for rabies antibody levels. Potentially virus-contaminated skin breaks, such as bites or scratches, should be scrubbed at once with soap and water, followed by irrigation with a virucidal agent. In these situations, tetanus prophylaxis and bacterial infection control may also be beneficial. Rapid initiation of laboratory tests on an animal source may indicate the species and **virulence** of lyssavirus, if present. The immediate initiation of antirabies globulin and vaccine treatments may be a lifesaving measure. However, some people have received treatment immediately and still died of rabies, having lost the race between the virus and immune-system response (Centers for Disease Control and Prevention, 2008). Nevertheless, rabies vaccines and globulin products approved for use in the USA are usually highly effective and reliable. It is important to note that tests to identify, and treatment for, exposures other than rabies or Australian bat lyssavirus may not be available or entirely satisfactory (Table 1).

Wildlife Rehabilitators

Among the many people who become wildlife rehabilitators are those who care for disabled bats. Because 1 in 10 disabled bats submitted for testing in the USA proves to have rabies, bat rehabilitators may avoid infection while handling bats by receiving inoculations of rabies vaccine. Rehabilitators may not emphasize the rabies hazard associated with bats during presentations given to school children or other audiences, because they may be motivated to care for and protect the reputation of bats and feel securely vaccinated. Complete presentations on the ecology of bats and their role in consequent rabies mortality may enhance audience appreciation of bats and educate them about the transmission of diseases carried by bats.

Table 10. Preemptive actions for minimizing human exposures to lyssaviruses.

Potential source for exposure	Preemptive actions
All bat species	
"Home deliveries" of bats by domestic cats	Vaccinate and confine cats. Control stray and feral cats.
Colonies of bats in manmade structures	
Schools	Prevent bat entry.
Other public contact sites	Prevent bat entry or post warning signs.
Colonies of bats in caves or mine tunnels	Prohibit entry to all but immunized persons with justifiable need for entry.
Flying bats observed entering buildings at night	Avoid contact and promptly facilitate ability of flying bat to exit building. Safely collect and submit non-flying bats for testing.
Unprovoked attacks by day-flying bats	Upon seeing flying bat, remain quiet and motionless until bat departs.
Vampire bats	
Colonies in human-inhabited areas	Destroy colonies using appropriate techniques.
Attacks on people	Educate susceptible human populations about vampire bat rabies and initiate appropriate protective measures, including vaccination and post-exposure treatment programs.
Attacks on livestock	Vaccinate livestock, employ protective husbandry of livestock, and institute vampire bat control programs.
Attacks on dogs and cats	Vaccinate pets, control their outdoor movements, and house pets indoors.
Attacks on other bats	Consider tropical bat bites, and other interactions between vampires and other bat species, as rabies exposures unless quickly proven otherwise.

Some rehabilitators may become embarrassed or fear consequent negative effects on their careers and on bats after they repeatedly submit rabid bats for testing. However, they need to know if a bat that has bitten them is infected so that they can receive vaccine boosters. Some rehabilitators ask friends to submit bats that bite, along with false histories, to distant laboratories for testing. Such actions may deprive the original discoverers of the bats of test results, and this knowledge is critical for the informed initiation of potentially lifesaving antirabies treatment.

Cave Explorers

Persons such as **speleologists** or biology students who contemplate entering bat harborages, including caves or mine tunnels, may be exposed to the health hazards associated with this activity and can take steps to decrease the risk of exposure. Applicable health hazards, precautions, and necessary preparations are detailed in a 38-page book chapter by Constantine (1988a). Topics covered include:

1. risks associated with exposure to pathogenic agents including rabies, rabies-related viruses, other viruses of bats, and histoplasmosis;
2. risks associated with exposure to bat urine, guano, and ectoparasites;
3. risks associated with oxygen deficit;
4. first aid and rescue concerning hazardous underground atmospheric gases such as ammonia, carbon dioxide, methane, carbon monoxide, and hydrogen sulfide;
5. risks associated with the deliberate contamination of bats or bat roosts with anticoagulants or poisonous gases;
6. recommended personal protective equipment; and
7. bat health problems caused by roost visitations.

Relevant preparation prior to cave exploration can save lives later. For example, carbon dioxide, which originates from various sources within underground caverns, including the exhalations of bats, is heavier than air and displaces oxygen, so it accumulates at lower underground levels where one may sit down to rest and soon become too weak to rise. Myotis bats show extraordinary resistance to **anoxia** (Britton and Kline, 1945), and Brazilian free-tailed bats can live in 100 times the ammonia concentration tolerated for five minutes by a human (Studier and others, 1967; National Institute for Occupational Health Standards, 1983). Therefore, the presence of live bats does not provide assurance that the atmosphere is safe for people.

Studies have shown that inhaled rabies virus enters nerve cells (olfactory receptor cells) that extend into the nasal cavity and are freely exposed to air as it is inhaled through the nose (Constantine and others, 1972). Accordingly, the virus essentially enters the brain as one inhales air. Airborne rabies transmission in the presence of massive Brazilian free-tailed bat aggregations within bat caves has been demonstrated (Constantine, 1967b), and similar aerosol transmission of other lyssaviruses and pathogens may be likely in similarly congested bat harborages, especially in tropical and subtropical zones. Fortunately, most explorers are repelled by these environments or undertake necessary preparations to ensure their safety and survival prior to entering. Pre-exposure rabies vaccination (Centers for Disease Control and Prevention, 2008) for all explorers of caverns known to harbor bats is an essential place to begin, but it may provide little or no protection against lyssaviruses other than rabies (Hanlon and others, 2005).

Animals

Recommendations for the prevention and control of animal rabies are available in the Compendium of Animal Rabies Prevention and Control (National Association of State Public Health Veterinarians, 2008). Information includes responses to known or potential exposures of domestic pets, such as dogs, cats, and ferrets, to rabid animals.

The prompt testing of bats that expose pet mammals is indicated, and if the bat is unavailable or unsuitable for testing, then it is prudent to assume that the bat is infected and that the animal was exposed to the virus. Exposed healthy pets with up-to-date vaccinations should be revaccinated immediately, kept under the owner's control, and observed for 45 days. Immediate euthanasia of an unvaccinated pet would ensure that disease is not transmitted to other animals or to humans. If euthanasia is not the first course of action for an unvaccinated pet, then it can be placed in strict isolation for 6 months and vaccinated upon entry into isolation or 1 month before release from isolation.

Domestic cats that are permitted to hunt and that bring home their victims account for the great majority of contacts between bats and humans and resulting human lyssavirus mortality. Because cat owners and their children are the foremost victims of lyssavirus transmission from pets, the relative ease and cost effectiveness of pet management would be likely to significantly decrease the problem (Box 9).

Clearly, much remains to be learned about lyssaviruses. For example, in an experimental case, a cat developed paralysis of its rear legs 17 days after it was inoculated with rabies virus from a big brown bat. The cat underwent gradual recovery until about 2 years later, when it suffered a relapse, became debilitated, and was euthanized, whereupon the virus was recovered from the cat's central nervous system (Murphy and others, 1980). This study discloses another method by which rabies virus can survive incognito over time, supplementing known incubation periods similar to dormancy in hibernating animals during the winter.

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Glossary

A

active immunity The internal capability of the body to combat disease agents; develops either following infection by a disease agent or by vaccination as the immune system responds by producing **antibodies** against the agent. (*See also* passive immunity.)

African bats Bat **species** native to the African continent.

Americas Lands of the New World (Western hemisphere), consisting of North, Central, and South America and their associated islands.

amphibians A group of **poikilothermic** ("cold-blooded"), scaleless, **vertebrate** animals that usually begin life in the water as gill-breathing tadpoles and that later develop lungs and spend part of their time on land.

amplification host A **host** in which infectious agents multiply to high concentrations, (*See also* intermediate host, reservoir host.)

anoxia A condition characterized by the absence of oxygen. For living organisms, this condition involves the absence of a supply of oxygen to an organ or a tissue.

antibody A protein formed in the body of a **vertebrate** that is used by the immune system to identify and neutralize the effects of foreign invading proteins, called antigens, such as bacteria and viruses. (*See also* maternal antibody, passive immunity.)

arthropods The largest group of animals, comprising more than 80 percent of described living animal **species**, that includes insects, spiders, and crustaceans. Arthropods are covered by a hard exoskeleton and are characterized by a segmented body, jointed legs, and many pairs of limbs.

B

bats **Mammals** in which the forelimbs have developed as wings, making them the only mammals in the world naturally capable of flight. There are estimated to be about 1,100 **species** of bats worldwide, accounting for about 20 percent of all mammal species. (*See also* African bat**.**)

> **insectivorous bats** Those that primarily feed on insects while in flight
>
> **fruit-eating bats** Those that feed almost entirely on fruit and on some green vegetation. (*See also* frugivorous.)
>
> **true vampire bats** Those that feed on blood obtained from animals and humans.

biological transmission Disease transfer requiring an **amplification host** (often an **arthropod**) for development or multiplication of the disease agent (or both) necessary for infection of another **host**.

biologics A range of pharmaceutical products including vaccines, blood components, and therapeutic proteins used to treat a variety of medical conditions.

birds Warm-blooded **vertebrates** with wings and feathers, although the wings are poorly developed in some **species** and they are flightless. Birds belong to the **taxonomic** class Aves.

blood serum The pale fluid that remains after blood has clotted.

burro A term used in the Western USA to refer to a **donkey**.

C

carnivores Animals whose diet consists mainly of meat.

clinical signs Readily observable indications of a disease or injury.

conspecific An organism of the same **species**.

cornea The transparent covering on the front of the eye.

D

dewlap A flap of skin containing stored fat that hangs beneath the lower jaw of animals including **mammals, birds, reptiles**, or **amphibians**.

DNA (deoxyribonucleic acid) A nucleic acid found mainly in the chromosomes that contains the hereditary information of organisms and some **viruses**.

donkey A pony-sized domesticated member of the horse family.

E

Ebola The common name for the **virus** that causes the fatal disease Ebola hemorrhagic fever. Ebola has caused a number of serious and highly publicized outbreaks since its discovery in Africa in 1976.

exsanguination The fatal process of total blood loss, or "bleeding to death."

F

flaccid paralysis Paralysis with a loss of muscle tone.

flying fox Large, fruit-eating bats with a fox-like appearance of the head. These **bats** are also commonly referred to as "fruit bats."

frugivorous An animal that feeds primarily or exclusively on fruit.

furious rabies A manifestation of rabies that in animals is characterized by periods of aggressive behavior towards inanimate objects and towards other animals and humans.

G

genet Small, largely nocturnal catlike **carnivores** with short legs, long bodies and tails, rounded ears, and pointed snouts; found in forests, savannahs, and grasslands of Africa and parts of Europe.

genotype The genetic makeup of a biological organism.

genus A **taxonomic** group of similar **species**; similar genera are grouped into families.

guano A term used here for the excrement of **bats**, but also including the manure of sea birds used as a fertilizer and other manure resembling the appearance of such excrements.

H

harp trap A large boxlike device effective for catching **bats**. A series of vertical wires extend upwards from the collection chamber. Bats in flight collide with the wires and then fall into the collection chamber below.

heterothermous An animal with the capability for regulating its internal body temperature above that of its environment during periods of activity. When the animal is at rest, however, its body temperature drops to that of its surrounding environment. (*See also* homoiothermous, poikilothermous.)

hibernation A state of inactivity in animals characterized by a lower body temperature, slower breathing, and a reduced metabolic rate. Hibernation allows animals to conserve energy during the winter when food may be unavailable.

histoplasmosis A potentially fatal disease that primarily effects the lungs and is caused by the fungus *Histoplasma capsulatum*. Spores of *H. capsulatum*, which are found in soil contaminated with bat or bird droppings, can become airborne when the contaminated soil is disturbed. Inhaling the spores can result in infection.

homoiothermous An animal with a body temperature that is constant and largely independent of the temperature of its surroundings. (*See also* heterothermous, poikilothermous.)

host An organism that harbors or nourishes microbes, **viruses**, and parasites. (*See also* intermediate host, reservoir host.)

hyperimmune sera Typically, **blood serum** with an especially high concentration of **antibodies** produced by repeated antigen injections into healthy donor **hosts**.

hypothermia A condition in which an animal's core body temperature drops below that required for normal physiological functions.

I

incubation period The time from the initiation of infection until the first recognized clinical signs.

insectivorous An animal that feeds primarily on insects.

intermediate host An organism in or on which a parasite develops for part of its life cycle. *(See also* host, reservoir host.)

J

jaguar The largest wild cat of the Americas. Typically found in thick wooded and arid shrubby environments from border areas of Texas and Arizona south to about 40° South latitude. A fierce predator, the jaguar is distinctly marked by black spots within the center of the rosettes that pattern its hide.

K

L

lyssavirus A **genus** of **viruses** of the family Rhabdoviridae.

M

mammals Warm-blooded **vertebrate** animals that possess hair during some part of their life and suckle their young.

maternal antibody An **antibody** transferred from a mammalian mother through the **placenta** into her fetus. (*See also* passive immunity**.**)

mechanical transmission Disease transfer involving contact with surfaces contaminated by **pathogens**. Mechanical transmission from bites, scratches, contact with inanimate objects, and other means allows disease-causing levels of the pathogen to enter the **host**.

Megachiroptera One of two **taxonomic** suborders of **bats** (the Chiroptera) and comprised of a single family, the Pteropodidae, or Old World fruit bats.

melancholia A nonspecific depression characterized by low levels of enthusiasm and low levels of eagerness for physical activity.

Microchiroptera The **taxonomic** suborder of **bats** (the Chiroptera) that contains all bats other than the **fruit bats** (**flying foxes**). It should be noted that some fruit bats (**Megachiroptera**) are smaller in size than some bat species within the Microchiroptera.

mites A medically important group of **arthropods** of the **taxonomic** order Acarina, but excluding ticks. These external parasites, closely related to spiders, cause a variety of infestations, often of the skin of humans and animals, and of the hair and feathers of animals.

monkeypox A viral disease related to smallpox that is transmissible between animals and humans and that primarily occurs in central and western Africa. The exotic pet trade resulted in the 2003 introduction of this disease into the USA.

mucosal surfaces Moist surfaces of orifices and internal parts of the body that cover, protect, and provide secretory and absorptive functions.

mule The usually sterile offspring of a male donkey and a female horse.

N

O

omnivorous An animal with a diet of both plants and animals.

P

paralytic rabies A manifestation of rabies that in animals is characterized by signs of posterior paralysis and that generally lacks the violent symptoms of **furious rabies**.

passive immunity Immunity achieved following the receipt of **antibodies** from an immune donor. Protection by passive immunity lasts for a relatively short time. For example, in humans, antibodies passed from mother to fetus confer passive immunity to the baby for the first 4 to 6 months of life. (*See also* active immunity.)

pathogen Typically, a mircoorganism capable of inducing disease, but broadly includes all disease-inducing agents.

placenta A temporary organ rich in blood vessels that transfers oxygen and nutrients from the mother to the fetus and that permits the release of carbon dioxide and waste products from the fetus. The placenta is expelled during the birth process.

plague An infectious disease of animals and humans caused by the bacterium *Yersinia pestis*. Although millions of people in Europe died from plague during the Middle Ages, modern antibiotics provide effective treatment of this disease when administered promptly following development of symptoms.

poikilothermous An animal with a body temperature that varies with the temperature of its environment. (*See also* heterothermous, homoiothermous.)

poultry A general term for farmed domestic birds, including chickens, turkeys, ducks, and geese.

prevalence The total number of cases of a disease in a population at a given time.

prodromal Early nonspecific symptoms, such as fever, headache, malaise, and nausea, indicating the start of a disease before specific symptoms occur.

putative Assumed or accepted as true.

Q

R

reptiles A group of poikilothermic ("cold-blooded"), air-breathing, **vertebrate** animals with scaled bodies. (*See also* poikilothermous.)

reservoir host An organism that maintains a disease agent in nature and that provides a source of infection to susceptible **hosts**. (*See also* intermediate host.)

S

salivary gland A gland that produces saliva.

sanguivorous An animal that feeds on blood; for example, certain bats, leeches, and insects.

serial transmission The sequential spreading of a disease agent among multiple susceptible **hosts**. (*See also* host.)

skunk Several species of **carnivores** within the family Mephitidae; specifically, the striped, hooded, spotted, and hog-nosed skunk.

species A population of organisms whose members are able to breed among themselves and produce fertile offspring. More precise determinations of species are based on similarity of **DNA**. (*See also* strain, variant.)

speleologist A person who explores caves.

strain A genetically or biochemically distinguishable subtype of a microorganism.

symptomatic Showing symptoms or signs of a disease or injury.

T

taxonomy The systematic principles and procedures of grouping and arranging organisms into a hierarchical order.

temperate zone Latitudes of the globe that lie between the tropics and the polar circles that exhibit seasonal temperature patterns.

torpid Dormant, as observed for hibernating animals. (*See also* hibernation.)

tropical Geographically, the zone on either side of the equator, bounded by the Tropic of Cancer (23°27' North latitude) and the Tropic of Capricorn (23°27' South latitude); climatically hot and humid for the majority of the year.

U

umbilical cord A tube that connects a developing embryo or fetus to the **placenta**.

V

vaccine A biological preparation containing an antigen, a molecule that stimulates the immune system, that is used to establish immunity to a disease.

variant A group of organisms of the same **species** that exhibit subtle yet characterizable differences from one another.

vector An animal, including insects, that carries a disease-causing organism from an infected to a healthy animal or plant, thus causing the latter to become infected.

vertebrates All animals that have spinal columns: **mammals, birds, reptiles, amphibians**, and fishes.

virulence The degree or ability of a pathogenic organism to cause disease. (*See also* pathogen.)

virus A microscopic infectious agent that can cause a disease, such as rabies in animals and potato virus in potato, tomato, and tobacco plants. A virus can reproduce only by invading living cells, and it exists outside of living cells as an inactive particle.

W

X

Y

Z

Zebu An Asian ox, domesticated and differentiated into many breeds, and physically distinguished from European cattle by the presence of a large fleshy hump over the shoulders, a loose skin prolonged in a **dewlap** and folds under the belly, and large droopy ears.

Appendix A. Bat Species Reported Infected with Rabies in the USA from 1953 to 2007

Bat species (common name)	Family
Big brown bat	Vespertilionidae
Big free-tailed bat	Molossidae
Brazilian free-tailed bat	Molossidae
California leaf-nosed bat	Phyllostomidae
California myotis	Vespertilionidae
Canyon bat	Vespertilionidae
Cave myotis	Vespertilionidae
Eastern red bat	Vespertilionidae
Evening bat	Vespertilionidae
Fringed myotis	Vespertilionidae
Gray myotis	Vespertilionidae
Greater bonneted bat	Molossidae
Hoary bat	Vespertilionidae
Keen’s myotis	Vespertilionidae
Little brown myotis	Vespertilionidae
Long-eared myotis	Vespertilionidae

Bat species (common name)	Family
Long-legged myotis	Vespertilionidae
Northern myotis	Vespertilionidae
Northern yellow bat	Vespertilionidae
Pallid bat	Vespertilionidae
Peter’s ghost-faced bat	Mormoopidae
Pocketed free-tailed bat	Molossidae
Seminole bat	Vespertilionidae
Silver-haired bat	Vespertilionidae
Southeastern myotis	Vespertilionidae
Southern yellow bat	Vespertilionidae
Spotted bat	Vespertilionidae
Townsend’s big-eared bat	Vespertilionidae
Tricolored bat	Vespertilionidae
Western red bat	Vespertilionidae
Western small-footed myotis	Vespertilionidae
Western yellow bat	Vespertilionidae
Yuma myotis	Vespertilionidae

Appendix B. Bat Species Reported Infected with Rabies in the Americas through 2006

Bat species (common name)	Family	Country where infection was identified
Argentine brown bat	Vespertilionidae	Brazil
Big brown bat	Vespertilionidae	Canada, Cuba, Mexico, United States
Big free-tailed bat	Molossidae	Brazil, Mexico, United States
Big-eared brown bat	Vespertilionidae	Chile
Black bonneted bat	Molossidae	Argentina, Brazil
Black mastiff bat	Molossidae	Brazil, Mexico, Venezuela
Black myotis	Vespertilionidae	Argentina, Belize, Brazil, Panama, Peru
Black-winged little yellow bat	Vespertilionidae	Mexico
Brazilian brown bat	Vespertilionidae	Colombia
Brazilian free-tailed bat	Molossidae	Argentina, Brazil, Chile, Mexico, United States
Broad-eared free-tailed bat	Molossidae	Brazil, Mexico
Brown fruit-eating bat	Phyllostomidae	Peru
Brown mastiff bat	Molossidae	Brazil
Bulldog bat	Noctilionidae	Panama
California leaf-nosed bat	Phyllostomidae	United States
California myotis	Vespertilionidae	Canada, United States
Canyon bat	Vespertilionidae	United States
Cave myotis	Vespertilionidae	Mexico, United States
Chilean myotis	Vespertilionidae	Chile
Cinnamon dog-faced bat	Molossidae	Brazil
Cinnamon myotis	Vespertilionidae	Belize, Guatemala
Common mustached bat	Mormoopidae	Mexico, Trinidad
Common sword-nosed bat	Phyllostomidae	Brazil
Common tent-making bat	Phyllostomidae	Panama
Common vampire bat	Phyllostomidae	Argentina, Belize, Bolivia, Brazil, Colombia, Costa Rica, Ecuador, El Salvador, Guatemala, Mexico, Nicaragua, Paraguay, Peru, Trinidad, Venezuela
Davy’s naked-backed bat	Mormoopidae	Mexico, Trinidad
Diminutive serotine	Vespertilionidae	Brazil
Eastern red bat	Vespertilionidae	Canada, Mexico, United States
Evening bat	Vespertilionidae	United States
Fringed myotis	Vespertilionidae	United States
Fringe-lipped bat	Phyllostomidae	Brazil
Fruit-eating bat	Phyllostomidae	Mexico, Peru

Bat species (common name)	Family	Country where infection was identified
Geoffroy's tailless bat	Phyllostomidae	Brazil
Gray myotis	Vespertilionidae	United States
Gray short-tailed bat	Phyllostomidae	Mexico
Great fruit-eating bat	Phyllostomidae	Belize, Bolivia, Brazil, Guatemala, Mexico, Peru, Trinidad
Great stripe-faced bat	Phyllostomidae	Brazil
Greater bonneted bat	Molossidae	Brazil, United States
Greater bulldog bat	Noctilionidae	Mexico
Greater spear-nosed bat	Phyllostomidae	Brazil, Peru
Hairy-legged vampire bat	Phyllostomidae	Brazil, Mexico
Hoary bat	Vespertilionidae	Argentina, Brazil, Canada, Mexico, United States
Jamaican fruit-eating bat	Phyllostomidae	Belize, Bolivia, Brazil, Grenada, Mexico, Panama, Trinidad
Keen's myotis	Vespertilionidae	Canada, United States
Lesser long-nosed bat	Phyllostomidae	Mexico
Lesser spear-nosed bat	Phyllostomidae	Peru
Little big-eared bat	Phyllostomidae	Brazil, Panama, Peru
Little brown myotis	Vespertilionidae	Canada, United States
Little yellow-shouldered bat	Phyllostomidae	Brazil
Long-eared myotis	Vespertilionidae	Canada, United States
Long-legged myotis	Vespertilionidae	United States
Mexican long-nosed bat	Phyllostomidae	Mexico
Northern ghost bat	Emballonuridae	Trinidad
Northern myotis	Vespertilionidae	Canada, United States
Northern yellow bat	Vespertilionidae	Mexico, United States
Pale spear-nosed bat	Phyllostomidae	Belize, Guatemala, Mexico
Pallas' long-tongued bat	Phyllostomidae	Mexico, Peru
Pallas' mastiff bat	Molossidae	Belize, Brazil, Colombia, Panama, Peru, Trinidad
Pallid bat	Vespertilionidae	Mexico, United States
Patagonian dwarf bonneted bat	Molossidae	Argentina
Peters' ghost-faced bat	Mormoopidae	Mexico, United States
Pocketed free-tailed bat	Molossidae	United States
Pygmy round-eared bat	Phyllostomidae	Brazil
Seba's short-tailed bat	Phyllostomidae	Colombia, Peru, Trinidad
Seminole bat	Vespertilionidae	Mexico, United States

Bat species (common name)	Family	Country where infection was identified
Silver-haired bat	Vespertilionidae	Canada, United States
Silver-tipped myotis	Vespertilionidae	Brazil
Sinaloan mastiff bat	Molossidae	Belize, Brazil, Guatemala, Honduras
Small big-eared brown bat	Vespertilionidae	Argentina
Southeastern myotis	Vespertilionidae	United States
Southern dog-faced bat	Molossidae	Panama
Southern yellow bat	Vespertilionidae	Brazil, Mexico, Paraguay, United States
Spotted bat	Vespertilionidae	Canada, United States
Tailed tailless bat	Phyllostomidae	Brazil
Thomas' mastiff bat	Molossidae	Panama
Townsend's big-eared bat	Vespertilionidae	United States
Tricolored bat	Vespertilionidae	Canada, Mexico, United States
Tropical big-eared brown bat	Vespertilionidae	Brazil
Wagner's bonneted bat	Molossidae	Cuba
Wagner's mustached bat	Mormoopidae	Mexico
Waterhouse's leaf-nosed bat	Phyllostomidae	Mexico
Western red bat	Vespertilionidae	Argentina, Brazil, Chile, United States
Western small-footed myotis	Vespertilionidae	Canada, United States
Western yellow bat	Vespertilionidae	United States
White-lined broad-nosed bat	Phyllostomidae	Peru
White-winged vampire bat	Phyllostomidae	Brazil, Mexico, Trinidad
Woolly false vampire bat	Phyllostomidae	Brazil
Yuma myotis	Vespertilionidae	Canada, United States

Appendix C. Common and Scientific Names for Species Cited

[Common and scientific names from Wilson and Reeder (2005)]

Common name	Scientific name
African shrews	*Crocidura* sp.
African straw-colored fruit bat	*Eidolon helvum*
Angolian free-tailed bat	*Mops condylurus*
Argentine brown bat	*Eptesicus furinalis*
Assassin bug	*Arilus cristatus*
Big brown bat	*Eptesicus fuscus*
Big-eared brown bat	*Histiotus macrotus*
Big free-tailed bat	*Nyctinomops macrotis*
Black bonneted bat	*Eumops auripendulus*
Black flying fox	*Pteropus alecto*
Black mastiff bat	*Molossus rufus*
Black myotis	*Myotis nigricans*
Black-winged little yellow bat	*Rhogeessa tumida*
Brazilian brown bat	*Eptesicus brasiliensis*
Brazilian free-tailed bat	*Tadarida brasiliensis*
Broad-eared free-tailed bat	*Nyctinomops laticaudatus*
Brown fruit-eating bat	*Artibeus concolor*
Brown mastiff bat	*Promops nasutus*
Bulldog bat	*Noctilio sp.*
Burro	*Equus asinus*
California leaf-nosed bat	*Macrotus californicus*
California myotis	*Myotis californicus*
Canyon bat	*Parastrellus hesperus* [1]
Cat (domestic)	*Felis catus*
Cattle (domestic)	*Bos taurus*
Cave myotis	*Myotis velifer*
Chilean myotis	*Myotis chiloensis*
Cinnamon dog-faced bat	*Cynomops abrasus*
Cinnamon myotis	*Myotis fortidens*
Common mustached bat	*Pteronotus parnellii*
Common pipistrelle	*Pipistrellus pipistrellus*
Common sword-nosed bat	*Lonchorhina aurita*
Common tent-making bat	*Uroderma bilobatum*
Common vampire bat	*Desmodus rotundus*
Crocidura shrew	*Crocidura sp.*
Daubenton's bat	*Myotis daubentonii*
Davy's naked-backed bat	*Pteronotus davyi*
Dermestid beetle	*Dermestes carnivorus*
Diadem leaf-nosed bat	*Hipposideros diadema*
Diminutive serotine	*Eptesicus diminutus*
Dog (domestic)	*Canis lupus*
Donkey	*Equus asinus*
Eastern red bat	*Lasiurus borealis*
Egyptian rousette	*Rousettus egyptiacus*
Egyptian slit-faced bat	*Nycteris thebaica*
Evening bat	*Nycticeius humeralis*
Ferret	*Mustela putorius*
Flying fox	*Pteropus* sp.
Fringed myotis	*Myotis thysanodes*
Fringe-lipped bat	*Trachops cirrhosus*
Fruit-eating bat	*Artibeus* sp.
Gambian slit-faced bat	*Nycteris gambiensis*
Genet	*Genetta tigrina*
Geoffroy's tailless bat	*Anoura geoffroyi*
Giant vampire bat	*Desmodus draculae*
Goat (domestic)	*Capra hircus*
Gray fox	*Urocyon cinereoargenteus*
Gray-headed flying fox	*Pteropus poliocephalus*
Gray myotis	*Myotis grisescens*
Gray short-tailed bat	*Carollia subrufa*
Great fruit-eating bat	*Artibeus lituratus*
Great stripe-faced bat	*Vampyrodes caracciolae*
Greater bonneted bat	*Eumops perotis*
Greater bulldog bat	*Noctilio leporinus*

Common name	Scientific name
Greater horseshoe bat	*Rhinolophus ferrumequinum*
Greater spear-nosed bat	*Phyllostomus hastatus*
Greater tube-nosed bat	*Murina leucogaster*
Hairy-legged vampire bat	*Diphylla ecaudata*
Hamster	*Mesocricetus auratus*
Hoary bat	*Lasiurus cinereus*
Horse (domestic)	*Equus caballus*
Indian flying fox	*Pteropus giganteus*
Jackal	*Canis adustus*
Jaguar	*Panthera onca*
Jamaican fruit-eating bat	*Artibeus jamaicensis*
Keen's myotis	*Myotis keenii*
Lesser dawn fruit bat	*Eonycteris spelaea*
Lesser long-nosed bat	*Leptonycteris yerbabuanae*
Lesser mouse-eared myotis	*Myotis blythii*
Lesser spear-nosed bat	*Phyllostomus elongatus*
Little big-eared bat	*Micronycteris megalotis*
Little brown myotis	*Myotis lucifugus*
Little free-tailed bat	*Chaerephon pumila*
Little red flying fox	*Pteropus scapulatus*
Little yellow-shouldered bat	*Sturnira lilium*
Long-eared myotis	*Myotis evotis*
Long-legged myotis	*Myotis volans*
Lyle's flying fox	*Pteropus lylei*
Mexican long-nosed bat	*Leptonycteris nivalis*
Mongoose	*Galerella sanguinea*
Mouse-eared myotis	*Myotis myotis*
Nathusius' pipistrelle bat	*Pipistrellus nathusii*
Noctule	*Nyctalus noctula*
Northern bat	*Eptesicus nilssonii*
Northern ghost bat	*Diclidurus albus*
Northern myotis	*Myotis septentrionalis*
Northern yellow bat	*Lasiurus intermedius*
Pale spear-nosed bat	*Phyllostomus discolor*
Pallas' long-tongued bat	*Glossophaga soricina*
Pallas' mastiff bat	*Molossus molossus*

Common name	Scientific name
Pallid bat	*Antrozous pallidus*
Particolored bat	*Vespertilio murinus*
Patagonian dwarf bonneted bat	*Eumops patagonicus*
Peter's ghost-faced bat	*Mormoops megalophylla*
Peter's lesser epauletted fruit bat	*Micropteropus pusillus*
Pig (domestic)	*Sus scrofa*
Pocketed free-tailed bat	*Nyctinomops femorosaccus*
Pond myotis	*Myotis dasycneme*
Pygmy round-eared bat	*Lophostoma brasiliense*
Queensland tube-nosed fruit bat	*Nyctimene robinsoni*
Red fox	*Vulpes vulpes*
Rhesus monkey	*Macaca mulatta*
Rusty-bellied brush-furred rat	*Lophuromys sikapusi*
Schreibers' long-fingered bat	*Miniopterus schreibersii*
Seba's short-tailed bat	*Carollia perspicillata*
Seminole bat	*Lasiurus seminolus*
Serotine bat	*Eptesicus serotinus*
Sharp-nosed tomb bat	*Taphozous georgianus*
Sheep (domestic)	*Ovis aries*
Shrew	*Crocidura* sp.
Silver-haired bat	*Lasionycteris noctivagans*
Silver-tipped myotis	*Myotis albescens*
Sinaloan mastiff bat	*Molossus sinaloae*
Skunk	*Mephitis* sp., *Spilogale* sp.
Small big-eared brown bat	*Histiotus montanus*
Southeastern myotis	*Myotis austroriparius*
Southern dog-faced bat	*Cynomops planirostris*
Southern yellow bat	*Lasiurus ega*
Spectacled flying fox	*Pteropus conspicillatus*
Spotted bat	*Euderma maculatum*
Stone martin	*Martes foina*
Tailed tailless bat	*Anoura caudifer*
Thomas' mastiff bat	*Molossus currentium*
Townsend's big-eared bat	*Corynorhinus townsendii*
Tricolored bat	*Perimyotis subflavus* [2]
Tropical big-eared brown bat	*Histiotus velatus*

Common name	Scientific name
Wagner's bonneted bat	*Eumops glaucinus*
Wagner's mustached bat	*Pteronotus personatus*
Wahlberg's epauletted fruit bat	*Epomophorus wahlbergi*
Waterhouse's leaf-nosed bat	*Macrotus waterhousii*
Water mongoose	*Atilax paludinosusis*
Western red bat	*Lasiurus blossevillii*
Western small-footed myotis	*Myotis ciliolabrum*
Western yellow bat	*Lasiurus xanthinus*
Whiskered myotis	*Myotis mystacinus*
White-lined broad-nosed bat	*Platyrrhinus lineatus*
White-winged vampire bat	*Diaemus youngi*
Woolly false vampire bat	*Chrotopterus auritus*
Yellow-bellied sheathtail bat	*Saccolaimus flaviventris*
Yuma myotis	*Myotis yumanensis*
Zebu	*Bos indicus*

[1] The canyon bat was formerly the Western pipistrelle (*Pipistrellus hesperus*). The species has been reclassified as the only member of the genus *Parastrellus* (Hoofer and others, 2006) and is currently referred to as the canyon bat.

[2] The tricolored bat was formerly the Eastern pipistrelle (*Pipistrellus subflavus*). This species has been reclassified as the only member of the genus *Perimyotis* (Menu, 1984; Hoofer and others, 2006) and is currently referred to as the tricolored bat.

Appendix D. Lyssavirus Infections in Bats Reported in Africa, Asia, Australia, and Europe

Common name	Family	Food habits	Geographic location	Lyssavirus species	Citation
African straw-colored fruit bat	Pteropodidae	Frugivorous	Nigeria Senegal	Lagos Lagos	Boulger and Porterfield, 1958 Markotter and others, 2006a
Black flying fox	Pteropodidae	Frugivorous	Australia	Australian	Warrilow and others, 2003
Common pipistrelle	Vespertilionidae	Insectivorous	Germany France	Unknown Unknown	WHO CCRSR,[1] 1988 Bruyère and Janot, 2000
Daubenton's bat	Vespertilionidae	Insectivorous	Denmark Germany Switzerland United Kingdom	EBL-2 EBL-2 EBL-2 EBL-2	Johnson and others, 2006 Johnson and others, 2006 Johnson and others, 2006 Johnson and others, 2006
Egyptian rousette	Pteropodidae	Frugivorous	Egypt	Lagos	Markotter and others, 2006b
Egyptian slit-faced bat	Nycteridae	Insectivorous	Zimbabwe	Duvenhage	Foggin, 1988
Gambian slit-faced bat	Nycteridae	Insectivorous	Senegal	Lagos	Markotter and others, 2006a
Gray-headed flying fox	Pteropodidae	Frugivorous	Australia	Australian	Warrilow and others, 2003
Greater horseshoe bat	Rhinolophidae	Insectivorous	Turkey	Unknown	Tunçman, 1958
Greater tube-nosed bat	Vespertilionidae	Insectivorous	Russia	Irkut	Botvinkin and others, 2003
Indian flying fox	Pteropodidae	Frugivorous	India	Unknown	Pal and others, 1980
Lesser mouse-eared myotis	Vespertilionidae	Insectivorous	Kyrghyzstan	Aravan	Botvinkin and others, 2003
Little red flying fox	Pteropodidae	Frugivorous	Australia	Australian	Warrilow and others, 2003
Mouse-eared myotis	Vespertilionidae	Insectivorous	Germany	Unknown	Hentschke and Hellman, 1975
Nathusius' pipistrelle bat	Vespertilionidae	Insectivorous	Germany	EBL-1	WHO CCRSR,[1] 1986
Noctule	Vespertilionidae	Insectivorous	Ukraine Yugoslavia	EBL-1 Unknown	Khozinski and others, 1990; Selimov and others, 1990 Nicolíc and Jelesíc, 1956

Common name	Family	Food habits	Geographic location	Lyssavirus species	Citation
Northern bat	Vespertilionidae	Insectivorous	Russia	Unknown	Khozinski and others, 1990; Selimov and others, 1990
Particolored bat	Vespertilionidae	Insectivorous	Ukraine	EBL-1	Kappeler, 1989
Peter's lesser epauletted fruit bat	Pteropodidae	Frugivorous	Central African Republic	Lagos	Sureau and others, 1980
Pond myotis	Vespertilionidae	Insectivorous	Denmark Netherlands	EBL-2 EBL-2	WHO CCRSR,[1] 1986 Van der Poel and others, 2003
Schreiber's long-fingered bat	Vespertilionidae	Insectivorous	Russia	WCBV	Botvinkin and others, 2003
Serotine bat	Vespertilionidae	Insectivorous	Russia Czech Republic. Denmark France Germany Hungary Netherlands Poland Spain Ukraine	Unknown Unknown EBL-1 EBL-1 EBL-1 Unknown EBL-1 EBL-1 EBL-1 Unknown	Amengual and others, 1997 Matouch, 1999 Amengual and others, 1997 Amengual and others, 1997 Amengual and others, 1997 Kerekes, 1999 Amengual and others, 1997 Amengual and others, 1997 Amengual and others, 1997 Selimov and others, 1986
Spectacled flying fox	Pteropodidae	Frugivorous	Australia	Australian	Warrilow and others, 2003
Wahlberg's epauletted fruit bat	Pteropodidae	Frugivorous	South Africa	Lagos	Crick and others, 1982
Whiskered myotis	Vespertilionidae	Insectivorous	Tajikistan	Khujand	Kuzmin and others, 2003
Yellow-bellied sheath-tail bat	Emballonuridae	Insectivorous	Australia	Australian	Warrilow and others, 2003

[1] World Health Organization Collaborating Centre for Rabies Surveillance and Research, Tübingen, Germany.

Appendix E. Course of Bat Lyssavirus Infections in Humans

Case 1. Exposure in South America (Hurst and Pawan, 1932)

The victim was awakened by being bitten on a toe of the left foot, whereupon a vampire bat was observed flying away from the foot.

Day 1 of symptoms, 27 days later: The victim felt a burning sensation and cramps in the left foot and was unable to flex the foot at the ankle. The left foot was also numb to touch. The symptoms later spread to the victim's leg, which became weak.

Day 3: The victim's right foot became numb. Symptoms grew worse over several days.

Day 7: The victim had flaccid paralysis and numbness in the left leg and right foot and numbness over the trunk to the level of eighth to ninth rib. The victim was unable to pass urine freely and had been constipated for the past 8 days. The victim could answer questions intelligently.

Day 8: The victim's symptoms became worse. The victim experienced slight breathing distress, some arm weakness, great thirst, and had a fever of 105°F (40.5°C).

Day 9: The victim experienced acute breathing distress, profuse sweating over the entire body, arm incoordination, and ascending numbness. Swallowing became impossible. The victim became semiconscious and died.

Case 2. Exposure in North America (Sulkin and Greve, 1954)

The victim picked up a grounded bat and was bitten on the forearm. The bat was discarded.

Day 1 of symptoms, 16 days later: The victim experienced aching of the forearms and developed a fever of 103°F (39.4°C).

Day 2: The victim felt generally achy, became nauseated and vomited, and one arm became paralyzed.

Day 7: The victim was unable to swallow and later became semicomatose to comatose.

Day 9: The victim's blood pressure decreased, and the victim died.

Case 3. Exposure in North America (Irons and others, 1957)

The victim was exposed to airborne rabies in a cave occupied by millions of Brazilian free-tailed bats.

Day 1 of symptoms, about 6 weeks later: The victim had visual problems that precluded driving. The victim reported a night of fitful sleep and nightmares.

Day 2: The victim had convulsive seizures while trying to drink water and the throat muscles became paralyzed. The victim also had breathing difficulties and acute anxiety.

Day 3: Symptoms grew worse, and supportive therapy was ineffectual.

Day 4: The victim died.

Case 4. Exposure in North America (Humphrey and others, 1960)

The victim picked up an injured silver-haired bat that was being attacked by dogs, placed the bat in a tree, and was bitten on the left forefinger. The victim was given antiserum 3 days later and started on vaccine 4 days after being bitten.

Day 1 of symptoms, 26 days after the bite: The victim's inner left arm became numb to the first two fingers. The victim's abdomen and spine became painful.

Day 8: The symptoms worsened, and numbness extended to the victim's arms. The victim was unable to urinate, then suffered overflow incontinence.

Day 9: The victim had poor limb muscle control and pain in many parts of the body. The victim was able to eat breakfast.

Day 10: The victim had severe leg and abdominal pain yet ate well.

Day 11: Symptoms became worse. The victim could not pass gas but ate well.

Day 12: The victim could not swallow mucus and felt heaviness in the chest. The victim died.

Case 5. Exposure in North America (Humphrey and others, 1960)

The victim was awakened by a bat biting his left ear lobe. A cat later ate the bat.

Day 1 of symptoms, 21 days later: The victim felt tingling and pain in the area of the left ear and had pain and tremors that spread to the neck and the left arm.

Days 5 and 6: After further deterioration, the victim had marked tremors in the left arm, prolonged muscle spasms of the legs and neck similar to those seen in cases of tetanus, and hydrophobic spasms when offered water.

Day 7: The victim died.

Case 6. Exposure in Europe (Lumio and others, 1986)

The victim was bitten by a Daubenton's bat that was acting abnormally. The bat was released.

Day 1 of symptoms, 51 days later: The victim's right palm was numb and felt pain in the neck.

Day 2: The victim's right cheek was numb and painful.

Day 9: The victim was unable to walk and felt generally weak. The victim's right arm and neck were numb, and the chest was painful.

Day 10: The victim developed muscle spasms of the jaw and the legs, prolonged rapid and deep breathing, throat spasms, facial grimacing, disturbed speech, swallowing difficulties, and dilated pupils. The victim exhibited overwhelming fear and was given antirabies serum and sedatives. Symptoms progressed to delirium with shouting, motor hyperexcitability, hypersalivation, and convulsions.

Day 11: The victim died.

Case 7. Exposure in Africa (Meredith and others, 1971)

The victim was awakened by a bat bite on the lip. The bat was destroyed.

Day 1 of symptoms, about 1 month later: The victim had headache, dizziness, and muscle aches in the neck and back.

Days 2 and 3: The victim sweated continuously and had muscle spasms in the face, arm, and leg. The victim became increasingly confused, irritable, and aggressive, had difficulty sleeping, and had nightmares. The victim's swallowing became progressively more difficult.

Day 4: All of the victim's reflexes became markedly exaggerated. When the victim attempted to drink, tremendous spasms of the mouth and throat muscles prevented swallowing and caused impaired breathing. Despite sedatives, the victim was tense, anxious, sweated profusely, and became increasingly violent and difficult to control. Upon further attempts to drink, the victim cried out in pain and had pharyngeal muscle spasms as well as spasms of the upper torso and arms.

Day 5: The victim went "completely berserk," frothing at the mouth and kicking at attendants, and had to be forcibly restrained. The victim had spontaneous uncontrollable spasms at decreasing intervals until the victim died during a seizure.

Case 8. Exposure in India (Veeraraghavan, 1955)

The victim chased boys from a grounded bat that they were pelting with stones. The victim then picked up the bat to place it in a tree, and the bat bit the victim's forearm, from which it was dislodged with great difficulty. The bat was discarded.

Day 1, about 11 weeks later: The victim's symptoms were not recorded.

Day 2 (perhaps later): The victim had severe general sickness, was restless, had difficulty swallowing, and regurgitated fluid that was in the mouth.

Days 3 and 4: The victim's condition deteriorated. The victim became very excited and restless and would shout, but could not explain why.

Day 5: The victim died.

Case 9. Exposure in Australia (Allworth and others, 1996)

The victim evidently became infected consequent to caring for fruit bats and experiencing a scratch or bite on an unknown date.

Day 1 of symptoms: The victim had pain and numbness in an upper limb.

Day 4: The victim's muscular control became uncoordinated. The victim had difficulty focusing, had shoulder pain, and vomited.

Day 6: After the victim's throat muscles became paralyzed, the victim was unable to swallow and breathe. The victim's condition continued to deteriorate.

Day 11: The victim became comatose.

Day 16: The victim died.

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Back cover photos (D.G. Constantine)

Top: A California leaf-nosed bat departing from a mine tunnel in the Sonoran Desert, California.

Bottom: A diadem leaf-nosed bat, Queensland, Australia.

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