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KEY FEATURES

- Bats are increasingly recognized vectors and reservoirs of zoonotic infections.
- Lyssavirus infections transmissible to humans by bats include Species 1 (classic rabies), 4 (Duvenhage), 5 and 6 (European bat lyssaviruses), and 7 (Australian bat lyssavirus).
- Vampire bats (Desmodontinae) transmit classic rabies to humans and domestic animals in Latin America.
- Insectivorous and frugivorous bats are vectors or reservoirs of Lyssaviruses Species 1, 4, 5, 6, and 7; Filoviruses (Ebola and Marburg); Henipaviruses (Hendra and Nipah); and some other viruses, bacteria, and fungi.
- Bat-transmitted rabies infections can be prevented by vaccination.
- Vampire bat rabies can be controlled by vaccinating the bats or killing them with anti-coagulants.

INTRODUCTION

The medical importance of bats (order Chiroptera) to human health is increasingly recognized. They are either proven or potential reservoirs and vectors of zoonotic human pathogens, especially viruses.1-5 Viruses from 24 different families have been detected in bats, often without obvious deleterious effects on their hosts, leading to the suggestion that peculiarities of their immune system may allow them to resist the effects of viruses that are highly pathogenic in other mammals, including human beings.4 Transmission may be direct, by bat bites or scratches, or through more subtle contact such as touching intact mucous membranes or inhalation of aerosol created by bats’ urine; or transmission may be indirect, by infecting other mammalian hosts, or by creating in their accumulated feces (bat guano), a culture medium for pathogenic fungi whose spores may be inhaled by people entering bat caves. Bats may damage fruit crops, and cattle and other domestic animals are vulnerable to bat-transmitted infections. In Latin America, vampire bat–transmitted bovine rabies (“der‐mengue”) and trypanosomiasis (“Trypanosoma evansi infection causing “surra”) threatens meat production. Nipah virus causes fatal disease in pigs in Southeast Asia, where epidemics have led to the culling of more than 1 million of these animals. Hendra, Menangle, and Tioman viruses have been responsible for fatal diseases in horses and pigs in Australia and Malaysia. However, bats are much less important, medically and economically, than rodents, although they host more zoonotic viral infections per species. Rats, mice, and voles are vectors and reservoirs of many prevalent zoonotic pathogens, such as Hanta and Arena viruses, plague bacillus, leptospires, rickettsiae, and parastrongyloids. Rodents also consume crops and food stores and damage human dwellings and installations. In their favor, bats are fascinating and beautiful animals that are protected and conserved in many Western countries and that benefit the environment by controlling insects, pollinating fruit trees, and distributing seeds. Bats are eaten medicinally in China and elsewhere, and as a delicacy and valuable source of protein in West Africa, Southeast Asia, Indonesia, New Guinea, and Australia (by native Australians). Catching and butchering bats and consuming inadequately cooked bats incur the risk of infection.

BAT BIOLOGY

Bats have a number of special characteristics, some of which are unique. They show extreme diversity, with their approximately 1100 species constituting 20% of all mammalian species, and they are widely distributed in all continents except Antarctica and some oceanic islands. Some species breed within the Arctic Circle. Bats are enormously abundant, sometimes occurring in colonies, flocks, or clouds composed of as many as 20 to 30 million individual animals. In caves inhabited by Mexican free-tailed bats (Tadarida brasiliensis), there may be more than 4000 bats/m³ in their cave roosts that accommodate up to 1 million bats. Bats are the only mammals capable of self-powered flying, as opposed to gliding. Some species migrate more than 1500 kilometers, and North American hoary bats (Lasiurus cinereus—Vespertilionidae) have reached Iceland and the Orkney Islands in the UK. The wing membrane is formed by the skin of the back and belly, and is supported by elongated fingers, externally rotated and adducted legs, and, in some cases, the tail. Some bats, such as true vampires, are also capable of quadrupedal gait. Most bats are nocturnal. They are the only vertebrates capable of catching insects in complete darkness, achieved by the use of sophisticated echolocation. Bats are variously insectivorous, frugivorous, flower-feeding, hematophagous, or carnivorous. Their weight ranges from 2 g in Craseonycteris thonglongai (the smallest of all mammals) to 1.6 kg in the largest species of Pteropus and Acerodon. Metabolic flexibility allows them to be heterothermic (extreme variation in body core temperature 2°C–41°C) and to hibernate. During flight, their body temperature rises above 38°C. They are the longest-living of tiny mammals (e.g., Myotis lucifugus, weighing only 7 g, has lived to 35 years). Bats roost, hanging upside down from their feet or clinging onto surfaces, in human constructions such as roof spaces, caves and attics of dwellings (bringing them into close contact with people), tombs, temples, mines, pipes, irrigation tunnels, and bridges, and in caves, rock crevices, foliage, tree cavities, trees, and bird and termite nests. Some species can fashion tent-like shelters out of leaves. Recently an epidemic of white-nosed syndrome has killed more than a million bats in the northeast United States and Canada. A cold-growing fungus, Pseudogeomyces destructans (“white-nosed syndrome fungus”) is the cause. Bats are infested with numerous ectoparasites, including bat flies, fleas, mites, ticks and Chimerus bugs.

The traditional classification of bats into suborders Megachiroptera and Microchiroptera was based on morphology and possession of echolocation by the latter. However, molecular phylogenetic studies support division into Old World Yinpterochiroptera (Pteropodiformes), including Pteropodidae and Rhinolophidae, and pan-global Yangchiroptera (Vespertilioniformes), including all the other families of bats. medically important species are members of both suborders: Pteropodidae (megabats, flying foxes, fruit bats, and rousettes; Figs. 140.1 and 140.2), horseshoe bats (Rhinolophidae), sheath-tailed bats (Emballonuridae), free-tailed bats (Molossidae, e.g., the Mexican free-tailed bat Tadarida brasiilensis mexicana (Fig. 140.3), moustache bats (Mormoopidae), slit-faced bats (Nycteridae, e.g., hairy slit-faced bat Nycteris hispida) (Fig. 140.4), New World
Species 1: (Classic) Rabies

In the Americas, this virus has been found in bats of the families Molossidae, Phyllostomidae [both in true vampire bats, Desmodontinae, and in non-vampire bats, such as Seba's short-tailed leaf-nosed bat (Carollia perspicillata; see Fig. 140.5)] and Vespertilionidae. It has been transmitted to humans by members of these families. In India, Species 1 was found in Pteropodidae, but transmission to humans has not yet been documented, although there has been a case of human rabies after a bat bite in Andhra Pradesh.

Species 2: Lagos Bat Virus

Lyssavirus Species 2 is grouped together with Species 3 Mokola virus (not found in bats) in Phyllogroup II. Although human disease has not been reported, direct or serologic evidence of Lagos bat virus (LGV) infection has been found in several species of fruit bats (Pteropodidae) in Africa: the very widely distributed straw-colored fruit bat (Eidolon helvum) that is often eaten as “bush meat,” epauletted fruit bats (Epomophorus, Epomops, and Micropteropus spp.), Egyptian rousettes (Rousettus aegyptiacus); and in vespertilionid species: long-winged bats (Miniopterus spp.) and Gambian slit-faced bats (Nycteris gambiensis). A new LGV-like lyssavirus (Shimoni virus) has been described in a leaf-nosed bat (Hipposideros species) in coastal Kenya. Seroprevalence of LGV is 30% to 70% in R. aegyptiacus and E. helvum. Serologic evidence of LGV-like infection was found in insectivorous and frugivorous bats in Cambodia.

Species 4: Duvenhage Virus

Lyssavirus Genotype 4 has been found in fruit bats, such as the Egyptian slit-faced bat (Nycteris thebaica—Nycteridae) (see Fig. 140.4) in Zimbabwe, the common bent-wing bat (Miniopterus schreibersii), and other vespertilionid species in east and southern Africa. The three identified human cases in South Africa and Kenya showed clinical features indistinguishable from classic rabies encephalomyelitis.

Species 5 and 6: European Bat Lyssavirus

This genotype is the only zoonotic virus in European bats. European bat lyssavirus (EBLV)-1 infection has been found in serotine bats (Eptesicus serotinus) and R. aegyptiacus, and EBLV-2 in Daubenton's bats (Myotis daubentoni), pond bats (Myotis dasycneme), and other Myotis spp. and greater horseshoe bats (Rhinolophus ferrumequinum).
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Fig. 140.4  Hairy slit-faced bat (*Nycteris hispida*—Nycteridae), Tsavo National Park, Kenya (© David A. Warrell).

Fig. 140.5  Seba’s short-tailed bat (*Carollia perspicillata*—Phyllostomidae) (© David A. Warrell).

Fig. 140.6  Common vampire bat (*Desmodus robustus*—Desmodontina) flying in a cave roost in Peru (© Dr. Ivan Vargas Meneses).

Fig. 140.7  Common vampire bat (*Desmodus robustus*—Desmodontina) showing cleft in lower lip for sucking up the blood meal (© Dr. Ivan Vargas Meneses).

Fig. 140.8  Common vampire bat (*Desmodus robustus*—Desmodontina) showing the enlarged thumb enabling quadrupedal gait (© Dr. Ivan Vargas Meneses).
Species 7: Australian Bat Lyssavirus

Genotype 7 Australian bat lyssavirus (ABL V) was first isolated from a black flying fox (Pteropus alecto) in New South Wales in 1996 and subsequently from three other species of flying fox (Pteropus poliocephalus, Pteropus scapulatus, Pteropus conspicillatus) and one species of insectivorous bat, the yellow-bellied sheath-tailed bat (Saccolaimus flaviventris—Emballonuridae). In 1996, two Queensland women died of diseases indistinguishable from classic rabies, one 5 weeks after scratches by an S. flaviventris and the other more than 2 years after bites by a flying fox. In 2012, a boy died after contact with a fruit bat. In the Philippines, ABL V has been found in Lyle’s flying foxes (Pteropus lylei) obtained from restaurants and in common bent-wing bats (Miniopterus schreibersii) and great round-leafed bats (Hipposideros armiger) in Cambodia and Thailand.

Other Rabies-Related Viruses

Phylogroup I: Aravan (Kyrgyzstan), Khujand (Tajikistan), Irkut (eastern Siberia, Russian Far East, northern China in greater tube-nosed bat [Murina leucogaster]), Ozernoe virus (Russian Far
factors X and IX (“draculin”), and activate plasminogen (“desmoteplase”—currently being developed as a thrombolytic drug, DSPA-alpha-1).

These anti-hemostatic factors ensure blood flow from the wound that the bat sucks up through a cleft in its protruded lower lip (see Fig. 140.7), underneath its tongue along paired ventral grooves. Predation is facilitated by vampire bats’ ability to clamber, hop, and spring using their hind legs and enlarged thumb (see Figs. 140.8 and 140.9). Vampire bats can regurgitate blood when they return to the roost, feeding not only their young and relatives but also other members of the colony—altruistic behavior that is unique among animals. Vampire bats roost in jungle caves (Fig. 140.14), hollow trees, and man-made tunnels and drains (Fig. 140.15).
communities of protective lighting, have led to small epidemics of human rabies transmitted by vampire bats. These have accounted for more than 500 deaths since 1975, usually affecting rural communities of indigenous Amerindians, such as the Warao in northeast Venezuela. There have been recent outbreaks in Colombia (Chocó, Santander) and Peru (Condorcanchi, Bagna, Puerto Maldonado, Ayacucho, and in 2016–2017, 85 human cases in Cuzco District), Brazil (Para, Maranhão), and Venezuela (Delta Amacuro). Humans are bitten at night on their extremities, ears, and faces. Children appear particularly vulnerable. They may not wake up but discover bleeding wounds showing a double puncture made by the incisors or a depressed lesion with a raised edge (Figs. 140.16 and 140.17) in the morning. Mosquito nets are normally protective, but accessible body parts may be attacked, and the vampire bat’s melena stool may be found staining the net (Fig. 140.18). Historical epidemics of vampire bat rabies, like the Trinidad cases, were characterized by predominantly paralytic disease, but a minority of patients develop hydrophobia and other features of furious rabies. Vampire bat–related strains of classic Species 1 rabies virus

Rabies Epizootics

Rabies (classic Species 1) is enzootic in many, but not all, vampire bat populations. Since the late 14th century, European explorers of the Caribbean and South America reported the association between vampire bat attacks and fatal human illness. From 1925 to 1936, there was an epizootic of vampire bat rabies in Trinidad, with 2000 fatalities in cattle and horses and 53 human deaths from the paralytic form of rabies. Initially, it was misdiagnosed as oleander poisoning, bulbar paralysis, botulism, or grass disease in the animals and poliomyelitis in the patients. Ecologic changes, such as destruction of forest and introduction of cattle ranching, construction of trans-Amazonian highways, the invasion of newly accessible jungle by gold miners, and electric power failures that deprived jungle

Fig. 140.12 Bite sites of vampire bats on a cow in Peru (© Dr. Ivan Vargas Meneses).

Fig. 140.13 Bite sites of vampire bats on a chicken in Peru (© Dr. Ivan Vargas Meneses).

Fig. 140.14 Natural cave roost for vampire bats in Peru (© Dr. Ivan Vargas Meneses).

Fig. 140.15 Irrigation drain used as a roost for vampire bats in Peru (© Dr. Ivan Vargas Meneses).
Prevention and Control of Vampire Bat Rabies

People, especially children, living in areas where vampire bat bites are common should, ideally, be protected by rabies pre-exposure immunization, but this is rarely practicable. However, the high risk of fatal rabies in affected communities (e.g., 16 of 57 people bitten by vampire bats in one village in northeast Brazil) reflects the inaccessibility of post-exposure prophylaxis. Bat-proofing of dwellings and sleeping under mosquito nets affords some protection, and electric house lighting may deter vampire bats. Vampire bats are highly susceptible to anti-coagulants, such as warfarin, which can be distributed to colonies by capturing the bats and releasing them after plastering them with warfarin paste. Treatment of cattle with controlled doses of warfarin will kill vampire bats feeding on them. Cattle can be vaccinated using adjuvanted Pasteur Virus strain vaccine, and the vampire bats themselves can be vaccinated with recombinant vaccinia-vaccine.

Non-Vampire Bat Rabies

In the United States, 30 of the 40 cases of human rabies reported between 1995 and 2008 were attributed to bat strains of Species 1 rabies virus. Fifteen were associated with *Lasionycteris noctivagans* or *Pipistrellus subflavus*, 11 with *Tadarida brasiliensis*, and 1 each with *Myotis* spp. and *Eptesicus fuscus*. However, there was a clear history of a bat bite in only a few of these cases, although some had been in direct contact with bats and others had bats in their homes. This suggests the possibility of subtle contact, such as the bat's licking an open wound or intact mucous membranes of a sleeping person. Bat strains of Species 1 appear more tolerant of low temperatures and are more able to replicate in endothelial cells than canine strains of Species 1. The recovery of two American children from bat-transmitted rabies encephalomyelitis may also suggest decreased virulence of bat strains. Aerosol transmission of rabies was claimed to explain infection of two visitors to Frio...
Caves in Texas inhabited by 20 to 30 million *T. brasiensis*, but it is far more likely that they were infected transdermally. In Asia, evidence of *Species 1* infection was found in insectivorous and frugivorous bats in Cambodia and China.

**Filoviruses: Marburg Virus and Ebola Virus**

The environmental reservoirs and vectors of these deadly hemorrhagic fevers have long been debated, but in Uganda, serologic and polymerase chain reaction evidence of Ebola and Marburg virus infections has been found in Egyptian fruit bats or rousettes (*R. aegyptiacus*), suggesting that this species may be a natural host of both viruses. Evidence of Lake Victoria Marburg virus has been found in *R. aegyptiacus* in Kitum Cave, Mount Elgon, Kenya, and Python and Kitaka Caves in Uganda—sites where humans have been infected. Touching bat feces and being hit by low-flying bats were identified as possible risk factors for acquisition of the infection. Insectivorous bats, such as greater long-fingered bats *Miniopterus inflatus* (Vespertilionidae), horseshoe bats (*Rhinolophus auchen),* and round leaf bats (*Hipposideros* spp., *Rhinolophidae*) have also been implicated in Gabon, Democratic Republic of Congo, and Uganda. In Democratic Republic of Congo, hunting of bats, such as migratory hammer-headed or big-lipped bats (*Hypsignathus monstrosus*, Pteropodidae) for human consumption was linked to the 2007 outbreak of Ebola virus. In the Philippines, Ebola virus Reston has been found in domestic pigs. Several asymptomatic human infections were reported. During the recent West African Ebola epidemic (2013–2016) involving more than 15,000 cases and more than 11,000 deaths, Angolan free-tailed bats (*Tadarida congoensis* or *Mops congoensis*) were implicated in infecting the index case in Melandou, Guinea, in December 2013. Three species of fruit bats, *Eidolon helvum*, *Hypsignathus monstrosus*, and *Rousettus aegyptiacus*, were implicated in the spread of infection.

**Paramyxoviruses (Nipah, Hendra, Menangle)**

There is phylogenetic evidence that bat paramyxoviruses were ancestors to all major extant paramyxoviruses, including measles, mumps, parainfluenza, respiratory syncytial virus, and important veterinary pathogens. Three emerging paramyxovirus infections have been described for which bats are the likely natural reservoirs, and domestic horses and pigs have proved to be the amplifying vectors for human infection. Hendra and Nipah viruses are Henipaviruses; Menangle is a Rubulavirus.

**Hendra Virus**

In 1994, there was an outbreak of fatal respiratory disease in horses and humans in Australia, attributed to a new pathogen, Hendra virus, whose natural reservoir is *Pteropus* spp. (*P. alecto*, *P. poliocephalus*, *P. scapulatus*, *P. conspicillatus*). Since 1994, there have been 60 outbreaks of Hendra in the northeastern coastal region of Australia, causing the deaths of 102 horses and four of seven human cases, including two veterinarians.

**Nipah Virus**

In 1998, there was an epidemic of encephalitis in Malaysia and Singapore affecting pigs and pig handlers in whom the case fatality was more than 40%. The causative virus, named Nipah after an affected village, is closely related to Hendra virus. *Pteropus vampyrus* and *Pteropus hypomelanus* are the natural reservoirs. In 2001 a geographically distinct strain of Nipah virus emerged in West Bengal and Bangladesh, causing respiratory as well as encephalitic symptoms, with subsequent annual outbreaks and case fatality of more than 74%. Transmission in the original Malaysia/Singapore epidemic was via infected pigs, whereas in India and Bangladesh it was by drinking infected date palm sap or by human-to-human contact. In 2018 there was a Nipah virus (Bangladesh lineage) epidemic in Kozhikode and Malappuram districts of Kerala, South India. There were 23 cases with a 91% case fatality rate. Apart from the index case, who was probably infected by a pet *Pteropus giganteus*, transmission was nosocomial, probably through aerosol spread by coughing. So far, more than 600 human cases of Nipah virus encephalitis have been diagnosed. The epidemics have been attributed to disruption of *Pteropus* ecology by deforestation (e.g., building the new Kuala Lumpur airport), which displaced the bats from their traditional roosts to agricultural areas where they have contact with domestic animals and humans. In Bangladesh and India, where there have been >150 deaths, human-to-human transmission within families has been inferred.

Menangle and Tioman viruses have been isolated from *Pteropus* spp. in Australia and Malaysia and from sick pigs. Influenza-like illness in pig farmers with Menangle seroconversion has been reported.

**Other Viruses**

Many of the other viruses that have been isolated from bats have not been proved to be either transmissible to humans, directly or indirectly, or to cause human disease. These include severe acute respiratory syndrome viruses, the Arenavirus ‘Tacaribe virus’, *Pteropine orthoreovirus* (formerly known as *Nelson Bay virus*), *Mojil dos Campos*, *Bimini*, *Catu*, *Guama*, *Manzanilla*, *Nepuyo*, *Oriboca*, *Montana myotis leukenesphelitis*, *Tamana bat*, *Mount Elgon bat*, *Entebbe*, *Astroviruses*, and *Bunyaviridae* (Hantan).

**Bacterial Infections**

*Lepostipria*, *Brucella*, *Bartonella*, *Coxiella* and *Rickettsia* spp. have been reported to occur naturally in bats. *Lepostipria*-infected bats are found in Asia and Europe, as well as the Americas. *Brucella* and *Bartonella* infections have been found in vampire bats in Brazil. Bats can be infected with enteric bacteria such as *Salmonella* spp. and *Escherichia coli*, but transmission to humans has not been reported. Transmission of Hansen’s disease (*Mycobacterium leprae*) by vampire bats has been suspected but not proven.

**Histoplasmosis**

Bat guano provides a rich medium for the growth of *Histoplasma capsulatum*; the environment in the bat roost fosters this growth. Humans exposed to dried guano have suffered massive infection and death by inhalation.

**Other Fungi**

Many other fungi have been found in association with bat roosts, including *Candida* and *Scopulariopsis* and *Geomyces* spp. (including white-nosed syndrome fungus of bats; see earlier), which can infect humans. The involvement of bats seems limited to the provision of a rich environment in the roost as a culture medium for these organisms.

**Protozoa**

*Trypanosoma evansi*, the causative agent of surra in domestic animals, has been demonstrated in vampire bats. These bats can mechanically transmit the trypanosome from host to host. *T. cruzi* has been reported also, but evidence for transmission to humans is lacking.

**PREVENTION OF BAT-TRANSMITTED INFECTIONS**

For measures against vampire bat rabies, see earlier sections. Ideally, bats and humans should not share the same microenvironment, but bats are rightly protected in many countries, and so expert
advice should be sought if they are found roosting in attics. An aggressive bat is likely to be unwell, perhaps rabid. All cases of scratches, bites, and possible mucosal contact should be reviewed for possible post-exposure rabies prophylaxis. Even the handling of a dead bat has been associated with transmission. Grounded, trapped, or sick bats should ideally be handled only by experts and never without gloves. The risk of inhaling aerosolized fungal spores and acquiring other bat-related diseases must be recognized by cave explorers (spelunkers) and prevented by wearing appropriate clothing and masks.

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