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Review

Bats as reservoirs of severe emerging infectious diseases

Hui-Ju Han[a,1], Hong-ling Wen[a,1], Chuan-Min Zhou[a], Fang-Fang Chen[a], Li-Mei Luo[a], Jian-wei Liu[a], Xue-Jie Yu[a,b,c,*]

[a] School of Public Health, Shandong University, Jinan 250012, Shandong Province, China
[b] Departments of Pathology and Microbiology and Immunology, University of Texas Medical Branch, Galveston, TX 77555-0609, USA
[c] Center for Biodefense and Emerging Infectious Diseases, University of Texas Medical Branch, Galveston, TX 77555-0609, USA

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ABSTRACT

In recent years severe infectious diseases have been constantly emerging, causing panic in the world. Now we know that many of these terrible diseases are caused by viruses originated from bats (Table 1), such as Ebola virus, Marburg, SARS coronavirus (SARS-CoV), MERS coronavirus (MERS-CoV), Nipah virus (NiV) and Hendra virus (HeV). These viruses have co-evolved with bats due to bats' special social, biological and immunological features. Although bats are not in close contact with humans, spillover of viruses from bats to intermediate animal hosts, such as horses, pigs, civets, or non-human primates, is thought to be the most likely mode to cause human infection. Humans may also become infected with viruses through aerosol by intruding into bat roosting caves or via direct contact with bats, such as catching bats or been bitten by bats.

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* Corresponding author at: University of Texas Medical Branch, Galveston, TX 77555-0609, USA. Tel.: +1 409 774 1786.
E-mail addresses: 201413941@mail.sdu.edu.cn (H.-J. Han), wenhonglingZ@sdu.edu.cn (H.-l. Wen), zcmsdu@163.com (C.-M. Zhou), chenfangfang5683@163.com (F.-F. Chen), jmsllm@163.com (L.-M. Luo), liujw_2012@163.com (J.-w. Liu), xuyu@utmb.edu (X.-J. Yu).
[1] Authors contributed equally.

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1. Introduction

Bats have been known to be reservoirs of Rabies virus for a long time (Pawan, 1959a,b), and bats have also been considered as natural hosts of many common human and animal viruses, such as measles, mumps, parainfluenza, canine distemper and hepatitis C viruses (Drexler et al., 2012; Quan et al., 2013). However, bats have caught our attention very recently, due to their association with several severe emerging infectious diseases. Currently, bats have been considered to be natural reservoirs of SARS-CoV, MERS-CoV, NiV, HeV, Ebola virus, and Marburg viruses. These viruses have attracted global attention in recent years for their severity and/or easy transmission. This article reviews special features of bats in viral transmission and maintenance, bat's role as the reservoirs of some important viruses, the methods for bat-borne viruses' transmission to humans, and ecological drivers of bat-borne emerging infectious diseases.

2. Special features of bats in viral transmission and maintenance

Bats belong to the order *Chiroptera* (Greek means Hand-Wing) and can be further classified into two suborders: the *Yinpterochiroptera* (*Megachiroptera*, commonly known as megabats) and the *Yangchiroptera* (*microchiroptera*, commonly known as microbats) (Simmons, 2005). Megabats eat fruit and microbats live on insects, small mammals, fish or blood. Megabats have no echolocation and microbats possess echolocation (except for *Rousettes* and its relatives) (Table 1).

Bats have many features that enable them to carry a diversity of viruses. With approximately 1240 recognized species worldwide, bats account for about 25% of all mammalian species, making them the second largest order of mammals (Jones et al., 2005; Turmelle and Olival, 2009). The huge diversity of bat species can provide a large breeding ground for viruses. In addition, bats are ancient species and can be traced back to 52.5 million years ago (Clyde et al., 2001; Jepsen, 1966). The long evolutionary history provides long period for a variety of viruses to co-evolve with bats to make bats their natural reservoirs. In order to facilitate flying, bats developed hollow bones to reduce body mass; as a result, they do not have bone marrow as other mammals to produce B cells. This special immunological characteristics of bats may enable bats to carry a large number of viruses without obvious illness (Dobson, 2005). During winter time, some bats hibernate to conserve energy. Reduced body temperature and metabolic rate may suppress immune responses and delay viral clearance from bats (George et al., 2011; Sulkin and Allen, 1974).

Some features of bats may keep viruses circulating among the bat population. Bats are social animals, millions of individuals can be found in a single cave. The large number of bats in a colony with physical proximity facilitates viral transmission among bats, maintaining viruses circulating stably among bats. A study showed that several emerging viruses could be amplified in a bat colony during the breeding season (Drexler et al., 2011). Microbats developed echolocation for navigation. Apart from ultrasonic waves, the vibration of the larynx can also generate aerosols, which may also play an important role in viral transmission among bats (Calisher et al., 2006).

Some features of bats can contribute to viral dispersal. With a large number of species, bats can be found in all continents except the Antarctica and inhabit various ecological niches, including trees, caves, and man-made structures, such as tunnels, deserted houses, even occupied houses in rural areas. The worldwide distribution and various habitats of bats pose the public to a general risk of infection with bat-borne viruses. Bats are special as the only mammals that can actually fly. Bats fly in their daily quest for food and seasonal migration, some of which can fly up to nearly 2000 km (Fleming and Eby, 2006). The ability to fly enables bats to carry viruses to distant areas. The eating behavior of bats can also be linked to viral transmission. Fruit bats cannot take a large amount of food, and to meet their demand for energy, instead of swallowing, they just chew to absorb sugars and higher energy components, and spit out the partially digested fruits. Discarded fruits contaminated by viruses in bat saliva may be eaten by other animals and infect them (Dobson, 2005). In addition, despite their small size, bats have a relatively long life span, most of the species live for 10–20 years and some can live up to 30 years (Brunet-Rossinni and Austad, 2004). The longevity of bats also increases the possibility of viral dispersal.

3. Evidence for bat origins of emerging infectious diseases

3.1. Hendra virus (HeV)

HeV (formerly known as equine morbillivirus) was first recognized in Australia in 1994, when it caused severe respiratory or neurological diseases in horses and humans (Murray et al., 1995). Many investigations were done in search for the natural reservoir of this new highly pathogenic virus. Initial screening of 2411 horses for HeV-specific antibodies showed negative results (Ward et al., 1996), and a later extensive serosurvey of 5264 sera from

Table 1
Summary for selective bat-borne viruses.

Virus	Putative host	Intermediate host	Modes of transmission	Drivers
Nipah virus	Flying foxes	Pigs	Close contact with the sick ones, drinking date palm juice contact with pigs	Climate changes, changes of farming practices (dual land use), transportation of pigs as merchandise, social/cultural practices, habitat destruction
Hendra virus	Flying foxes	Horses	Contact with horses	Climate changes, Urbanization, Social/cultural practices
SARS-CoV	Horseshoe bats	Palm civets	Slaughtering, farming of wildlife	Economic growth, desire for game meat, wildlife trading in wet markets, international travel
MERS-CoV	Bats[a]	Dromedary camels	Direct contact with camels, consumption of camel milk/meat	Not known
Ebola virus	Egyptian fruit bats	Non-human primates	Slaughtering, hunt for bush meat,	Preference for bush meat, burial practices, poor healthcare practice

[a] Specific bat species not identified.