Bat's Role in Emergence and Spillover of Viral Zoonotic Diseases: A Review

H. Malik¹, S. Kaur¹, R. Singh¹

, N. Parmar¹**10.18805/ag.R-2590**

ABSTRACT

Several human infections have emerged in the last three decades, most of them are attributed to wildlife origin. Two third of the emerging zoonotic infections are attributed to viruses. Emerging and re-emerging fatal viral diseases like Nipah virus disease, Hendra Virus disease, Severe Acute Respiratory Syndrome, Middle East Respiratory Syndrome, Ebola and Marburg haemorrhagic fever have been witnessed recently, causative agents of which have been associated with bats. Ecology of bats influences the hostpathogen interaction and is responsible for harbouring several viruses, which under favourable conditions spill over to intermediate hosts. Conditions and events, such as deforestation, agricultural and livestock practices, animal migration and trade, eco-tourism, urbanization and other anthropogenic factors, greatly influence the successful interspecies transmission and emergence/re-emergence of zoonoses. This review highlights, the bats ecological factors and human-bat interface, responsible for zoonotic outbreaks in past. The implementation of an integrated approach is needed for unravelling the host-virus dynamics as well as providing mutually beneficial solutions for bat conservation and safeguarding animal and public health at a global level.

Key words: Bat ecology, Bats, Emerging, Re-emerging, Spill-over, Viral zoonoses.

Bats are classified under order Chiroptera because of their winged limbs and ability to fly. These are the second most abundant and diverse mammalian species on earth after rodents. Bats, which evolved around 52 million years ago, comprise more than 1200 identified species (Jones *et al*., 2005). These are classified under 175 genera arranged in 20 families (Schmid *et al*., 1993). Based on echolocation and feeding habits, these are classified under two major suborders, Yinpterochiroptera and Yangchiroptera. Yinpterochiroptera bats are microbats, which feed on insects and use echolocation for navigation. Whereas, frugivorous megabats are classified under Yangchiroptera, which do not use echolocation for navigation, instead, they have large light-sensitive eyes for navigation (Fenton, 2010). Due to their powerful flight, bats are distributed worldwide except Antarctica and a few other polar regions. Despite being instrumental in the ecosystem for pollination, soil fertility and pest control, bats are disreputable for being natural reservoirs for numerous pathogens notably zoonotic pathogens which get transmitted to other species on various occasions. In the past decade, the number of emerging zoonoses and geographic distribution of previously known zoonotic pathogens has been increased tremendously.

Around 75% of emerging zoonotic pathogens are associated with wildlife reservoirs (Daszak *et al*., 2000; Jones *et al*., 2008) and 66% are attributed to viruses (Woolhouse *et al*., 2007). Surveillance data documented in bat database DbatVir, which was collected from 196 bat species in 69 countries worldwide, illustrates 4176 batassociated animal viruses of 23 virus families (Chen *et al*., 2014). Around 43% of emerging and re-emerging pathogens listed as bioterrorism agents of category A, B and C are

¹Centre for One Health, Guru Angad Dev Veterinary and Animal Sciences University, Ludhiana-141 004, Punjab, India.

Corresponding Author: R. Singh, Centre for One Health, Guru Angad Dev Veterinary and Animal Sciences University, Ludhiana-141 004, Punjab, India. Email: sainirandhir74@gmail.com

How to cite this article: Malik, H., Kaur, S., Singh, R. and Parmar, N. (2023). Bat's Role in Emergence and Spillover of Viral Zoonotic Diseases: A Review. Agricultural Reviews. doi:10.18805/ag.R-2590 **Submitted:** 13-09-2022 **Accepted:** 27-03-2023 **Online:** 31-05-2023

recognised in different bat species (Beena, 2019). Bats species have emerged as potential reservoirs for numerous and diverse zoonotic pathogens, most notably virulent RNA viruses, which can cross barriers and infect humans, livestock and other wild animals (Brook, 2015). One of the oldest zoonotic virus-associated to bats is lyssavirus and the recent ones include rapidly emerging zoonoses like Severe Acute Respiratory Syndrome, Middle East Respiratory Syndrome, Nipah and Hendra viral diseases and re-emerging zoonoses like Ebola and Marburg viral diseases, which are also attributed to bat origin (Calisher *et al*., 2006). Besides, the ongoing pandemic COVID-19 caused by a novel coronavirus, SARS-CoV-2 is probably originated from bat coronaviruses (Zhou *et al*., 2020).

Ecological factors allow bats to harbour pathogens

The ecology of bats has been reported to play a major role in the emergence and maintenance of new viruses and their further spillover. Bats' unique and diverse modes of life, in particular, their flying ability, gregarious social structure, hibernation and their ability of torpor, differentiate them from all the other sylvatic disease reservoirs. These features affect the host-pathogen interaction, infection dynamics and also influence the spillover of the pathogen from bats to other host species.

Seasonality

Bats from temperate regions adopt mechanisms like migration, hibernation, restriction of birth periods, gregarious colonies and torpor to sustain in the cold seasons. These seasonal dynamics of the host have been associated with the seasonality of the pathogen prevalence and infection occurrence (Altizer *et al*., 2006). Prevalence of the coronavirus, astrovirus and adenoviruses in bat colonies is significantly affected by seasonality and breeding success (Drexler *et al*., 2011). More than 80% of the human infections of Marburg viral diseases were found to occur in the seasonal birth period of *Rousettus aegyptiacus* bats *i.e.* from becoming pregnant to giving birth biannually from November to February and May to August (Amman *et al*., 2012). The prevalence of rabies in Brazillian free-tailed bat colonies was significantly associated with seasonal fluctuations after parturition (Turmelle *et al*., 2010). Hendra virus also exhibits similar seasonality trends, winter spillover events in Queensland and New South Wales (Giles *et al*., 2018). Detection of astroviruses in bat colonies was also observed more during rainy season as compared to dry season (Seltmann *et al*., 2017).

Host reproduction and survival

Highly synchronised summer reproduction pulse in bat colonies brings several females in close contact and an influx of susceptible young ones doubles the population in a confined space for a short period. Interaction among adult bats and with the pups during lactation maintains and transmit the virus in the colony over generations. Correlation between virus amplification (coronavirus, astrovirus, filovirus and adenovirus) and bat population after parturition suggests the role of susceptible young hosts in maintaining the infection dynamics (Hayman *et al*., 2010; Drexler *et al*., 2011; Hayman *et al*., 2012).

Migration

Bat colonies of temperate regions either hibernate during winters or migrate to tropical regions in search of food (Fleming, 2010). During migration, contact among bat colonies facilitates the inter-colony exposure of diverse pathogens resulting in immunity against them (Paweska *et al*., 2015). Bat population density and their contact rate influence the pathogen prevalence and spillover (Hayman *et al*., 2013). For instance, the migration of fruit bats to urban dwellings in search of food increased the contact among resident bat colonies which shows a correlation between the bat migration and spillover of Nipah virus in Malaysia (Looi *et al*., 2007). In contrast, a spatial and temporal exploratory model predicted that reduced migration in bat colonies hampers their immunity and may cause fulminant growth, spillover and intense outbreaks of Hendra virus after reintroduction locally (Plowright *et al*., 2011).

Torpor

During unavailability of food or under physiological stress conditions, bats compensate their energy and water requirement by undergoing deep or shallow torpor in temperate and tropical regions, respectively (Hayman *et al*., 2013). Reduced host metabolism lessens the clearance of the pathogen, increases the incubation period and decreases mortality resulting in persistence of the pathogen in the host and maintenance within colonies by close contact. Pathogens reactivate on arousal from the torpor and multiply actively increasing the risk of spillover (Gerow *et al*., 2019). The perpetuation of lyssavirus in bats during torpor by lowered immunity, low viremia and subsequent shedding after arousal has been established (George *et al*., 2011).

Long life span

Bats are known to live longer than other mammals of comparable body size. Traits like hibernation and flying ability are hypothesised to be the reasons for their longer lifespan (Wilkinson *et al*., 2002). Though maximum age of bats varies from species to species yet they can live for 25 to 30 years (Moratelli *et al*., 2015). Certain bat species like *Myotis brandtii* is reported to even live for 41 years (Wilkinson *et al*., 2002). This also enables the bats to shed the pathogens for a long time and on various occasions thereby influencing disease dynamics.

Flying ability

An increase in metabolic rate and core body temperature in bats during flight activates their immune system. This routine increase in body temperature by flight explains the evolution of pathogens exhibiting resistance towards the immune system and their persistence without overt signs of illness (O'Shea *et al*., 2014).

Immunological tolerance

Bats' immune system allows them to harbour highly pathogenic viruses without showing overt signs of illness. Many studies revealed a deep phylogenetic relationship between bat species and various virus families including lyssavirus, paramyxovirus, coronavirus, filovirus, astrovirus, adenovirus and hepadnavirus (Brook *et al*., 2015). A study revealed that the immune system of bat adopts different mechanisms for control of RNA and DNA viruses. For RNA virus seasonal amplification in insectivorous bat colonies has been observed during colony formation and parturition, however, this is not observed for DNA viruses (Drexler *et al*., 2011). RNA viruses are found to survive and maintain viral load in bats by suppressing inflammatory responses mediated by Nod-Like Receptors family pyrin domain 3 (NLRP3) in bat primary immune cells, by reducing the ability to produce inflammatory cytokine, IL1 β (Ahn *et al.*, 2019). Studies have demonstrated rapid transmission of viruses in bat cell lines. This behavior enables them to evade the immune responses in naturally infected bats and exhibit increased virulence when infecting other mammalian species (Brook *et al*., 2020). Inflammatory response pathways against exogenous and self DNA are also dampened in bats. The receptors of PYHIN (Pyrin and HIN domain) family have been negatively selected for and lost in the genomic sequences of bats. Interferons (IFN) stimulator genes are less functional in bat cells (Banerjee *et al*., 2020).

Drivers for disease transmission

A successful interspecies transmission depends on various conditions and events, for instance the presence of infection in bats, infectivity and stability of the pathogen, shedding of sufficient dose of pathogen and presence of the susceptible hosts. Despite all, the most crucial event for spillover is the interaction between the infected bats and susceptible animals or humans, by sharing the same habitat. However, it has to be realized that biological ecosystems are complex and driven by multiple factors simultaneously (Fig 1), such as:

Expanding human population

Continuously increasing population demands the expansion of human settlement to uninhabited areas which leads to forest encroachment and habitat destruction of various wild species making the environment conducive for increased wild-human interface and pathogen spillover. It was observed that habitat destruction pulled the bat population near animal farms and human habitats which infected livestock animals and concurrently triggered the outbreaks of Hendra and Nipah viruses in Australia and Malaysia, respectively (Field *et al*., 2001). Analysis of few previous outbreaks of rabies in the human population in Peru and Brazil around 1900, revealed the reoccurrence of anthropogenic activities such as deforestation and gold mining in most outbreaks (Schneider *et al*., 2009).

Agricultural practices and livestock farming

An exponentially expanding population poses a threat to global food security and demands for intensive agriculture and animal husbandry practices. The integrated animal farms and agricultural patches not only promise an abundant supply of food for the uninhabited bat population but also bring different species in close contact disrupting the species barrier for the pathogen transmission. Studies show that the emergence and high prevalence of pathogens in livestock coincide with the occurrence of epidemics and pandemics. One such example is the first outbreak of Nipah virus, associated with intensive pig farming, in Ipoh, Malaysia in 1998 (Chua *et al*., 1999). Other instances of outbreaks of Ebola virus and Rabies virus in Central Africa and Latin America were associated with the intensification of agriculture patches and animal farms, inviting frugivorous bats and haematophagous bats close to humans and domestic animal (Greenhall *et al*., 2018).

Bush-meat hunting

Recreational activities, traditional practices, poor socioeconomic conditions and food insecurity demand humans to hunt and consume bush meats. Bushmeat handling and consumption have been linked to the emergence of outbreaks in the past. Transmission occurs by droplets and contact while slaughtering of the game and also by consumption of raw or undercooked meat. Ebola virus outbreak in the Democratic Republic of Congo in 2007 is the best fitting example here (Leroy *et al*., 2009).

Illegal trade of wildlife

Highly lucrative market in wildlife trade, for consumption, medicines (Mildenstein *et al*., 2016) and as souvenirs (Lee *et al*., 2015), encourages illegal hunting and trade of wildlife, exposing a large number of people involved in hunting and marketing chain. Trade of wild species in Asian markets brings multiple exotic species in close contact and allows

Fig 1: Drivers for disease transmission in bat colonies and then to human population.

the emergence and spread of novel viral diseases like SARS (Drexler *et al*., 2011) and COVID 19 (Li *et al*., 2020). Huanan wet market in Wuhan is allegedly responsible for the emergence and transmission of SARS-CoV 2, the causative agent for an ongoing pandemic of COVID 19.

Trade

Globalization facilitates the trade of animals and goods across the world and enhances the introduction of new pathogens in countries. Trade of pigs from Malaysia to Singapore carried the Nipah virus from one country to another causing a massive outbreak (Chua, 2000). Trade of wild species in Asian markets brings multiple exotic species in close contact and allows the emergence and spread of novel viral diseases like SARS and COVID 19.

Travel and tourism

International and local travels make the disease containment difficult in these times. Pandemics of COVID 19 and SARS in past years have illustrated the role of quick international travels in disseminating the infectious agents worldwide in a very short span of time. Tourism to exotic places for recreational activities and eco-adventure is gaining popularity and likewise increasing more wildlife-human interactions. Occurrence of Marburg hemorrhagic fever to an American tourist in December 2007 and then to a Dutch tourist in July 2008, after visiting Python caves in Uganda, is appropriate to state here (Timen, 2009).

Urbanization

Urbanization not only prevents the exposure of humans to the natural ecosystem but increases human to human contact in crowded places, making the environment more conducive for the dissemination of infectious agents. Close contact with bats dwelling in human shelters make humans even more susceptible and vulnerable to the disease. A model describes the role of urban habitation and decreased migratory behavior of bats (due to continuous availability of food and shelter) on frequent virus spill-over events. This was evident from the fact that occurrence of 10 out of 14 Hendra virus outbreaks occurred in communities in Australia which were continuously inhabited (Plowright *et al*., 2011).

Evidence of bat-borne zoonotic viruses

Lyssaviruses

Rabies virus is one of the oldest and most significant zoonotic pathogens in the history of mankind. All 14 species of lyssaviruses have been isolated from bats except the Mokola virus (Nel *et al*., 2007). Phylogenetic analysis and virus-host relationship suggest that bats have been the reservoir for all lyssaviruses from ancient times. There are 14 identified species of lyssavirus which are divided into three phylogenetic groups. Group-I includes Rabies virus (RABV), European bat lyssavirus 1 (EBLV-1), European bat lyssavirus 2 (EBLV-2), Aravan virus (ARAV), Duvenhage virus (DUVV), Khujand virus (KHUV), Australian Bat lyssavirus(ABLV), Irkut Virus (IRKV) and Bokeloh bat lyssavirus (BBLV); group II includes Lagos bat virus (LGV), Mokola bat virus (MOKV) and Shimoni bat virus (SHIBV) while group III includes only two species, West Caucasian Bat virus (W CBV) and Lleida bat lyssavirus (LLEBV) (Badrane *et al*., 2001; Banyard *et al*., 2014). From ancient times, Vampire bats were considered to transmit the Rabies virus to humans and livestock, but in the 1950s other species of insectivorous bats were also identified to transmit RABV in Northern and Southern America (Baer *et al*., 2017). European Bat lyssavirus was first isolated from a rabid bat in the year 1954. EBLV1 was divided into two different lineages of which EBLV1a is detected in northern Europe, however, EBLV1b has a more widespread distribution in Europe. EBLV 2 was isolated from *Myotis* spp*.* bat in the Netherlands and is prevalent in Northern Europe. Clinical presentation of human infection by EBLV2 was found similar to RABV, but was found less virulent than EBLV1 (Harris *et al*., 2006). Lagos bat virus was first isolated in the year 1956 in Nigeria but was not linked with the Rabies virus until 1970 (Shope *et al*., 1970). Duvenhage virus was first isolated from a human who died of a bat bite in the year 1970 (Meredith *et al*., 1971). In India, a 5.1% prevalence of rabies neutralizing antibodies have been reported from bats in Nagaland hills, suggesting prior exposure to RABV or other lyssavirus species (Mani *et al*., 2017).

Filoviridae

Filoviruses, including Ebola and Marburg virus, cause outbreaks of haemorrhagic fever characterized by a human to human transmission and significantly high mortality rates. Marburg virus was first described in the year 1967 following two haemorrhagic fever outbreaks in Germany and Serbia lab-workers after handling infected African green monkeys imported from Uganda. After a gap of eight years, a few Marburg outbreaks, associated with cave visits, occurred in Africa but a reservoir host for the virus was not established (Conrad *et al*., 1978; Johnson *et al*., 1996). It was only during the years 1988-2000, that the outbreaks, which occurred in workers of gold mines inhabited by bat population provided stronger evidence of bats acting as a reservoir for Marburg virus, based on DNA homology between human and bat Marburg viruses (Brauburger *et al*., 2012). The index case of Marburg outbreak in Uganda was also traced back to Kitaka mines (Towner *et al*., 2009). In 2007, a large outbreak of ebolavirus occurred in the DRC with 71% mortality, where the index case was associated with the consumption of fruit bats (Leroy *et al*., 2009). Also in 2008, two tourists who visited Python caves developed Marburg disease (Timen, 2009; Brauburger *et al*., 2012). A large number of seroprevalence studies on a wide range of bats in Ghana, Gabon, China, Bangladesh, Philippines and other African regions demonstrated frugivorous and insectivorous bat species as the reservoirs of virus (Leroy *et al*., 2005; Pourrut *et al*., 2009; Hayman *et al*., 2012; Yuan *et al*., 2012; Olival *et al*., 2013; Jayme *et al*., 2015). In 2014, the largest outbreak of Ebola haemorrhagic fever occurred in Sierra Leone, Guinea

and Liberia, with Zaire ebola virus strain causing a 70% mortality rate. Three fruit bat species, namely the hammerheaded fruit bat (*Hypsignathus monstrosus*), the little collared fruit bat (*Myonycteris torquata*) and the strawcoloured fruit bat (*Eidolon helvum*) were found associated with the outbreak (Alexander *et al*., 2015). A study from the Northeast region of India reported the presence of filovirus reactive antibodies in humans as well as fruit bat populations without any overt clinical disease (Dovih *et al*., 2019).

Paramyxoviridae

Genus *Henipavirus* in paramyxoviridae includes two members, Hendra virus (HeV) and Nipah virus (NiV), each causing severe respiratory illness and neurological disease in humans and animals. Hendra virus (HeV) was first identified in 1994, which caused illness and death in horses and close contact humans in Brisbane, Australia (Murray *et al*., 1995) (Table 1). While incidence and infectivity of virus is low, the case fatality of the virus is high which claimed 55 horses from 62 (80%) infected and 4 of the 7 (54%) infected humans (Field *et al*., 2011). Evidence of infection was found in all four species of fruit bats of genus *Pteropus* (*Pteropus alecto*, *P. conspicillatus*, *P. poliocephalus*, *P. scapulatus*) in Australia, establishing them as a reservoir host for the virus (Young *et al*., 1996). These bats were found to shed the virus in urine and uterine excretions.

Another member of henipavirus, Nipah virus (NiV-M), was first identified to cause severe respiratory illness and neurological manifestations in intensively reared pigs and associated humans in 1998-99 in Malaysia and Singapore. The outbreak claimed 105 lives of 265 infected humans and nearly one million pigs were culled as a preventive public health measure (Chua *et al*., 1999). Seroprevalence in five species of bats as well as virus isolation from urine and partly eaten fruits by *Pteropus hypomelanus* confirmed the role of bats as reservoir hosts (Yob *et al*., 2001; Chua *et al*., 2002). Later in 2001, a different strain of Nipah virus (NiV-B) was identified to cause an outbreak in Bangladesh and India, where initial cases were associated with the consumption of date palm sap contaminated by *Pteropus medius* saliva (Luby *et al*., 2006) and subsequently human to human transmission was reported (Hegde *et al*., 2016). A total of 211 deaths from 280 infected humans have been reported from the region so far (Herriman, 2019).

Recently, in 2018, another outbreak of Nipah occurred in Kerala, infecting 23 people and taking 21 lives (89%CFR) (Plowright *et al*., 2019). Phylogenetic analysis of virus revealed ~96% similarity with NiV-B and ~99% similarity with Nipah virus isolated *Pteropus* spp., confirming bats as a source of the outbreak (Yadav *et al*., 2019). Studies have reported viral RNA and neutralizing antibodies for NiV-B in bats captured from different states of India (Epstein *et al*., 2008; Yadav *et al*., 2012; Plowright *et al*., 2019). Prevalence and seroprevalence studies demonstrate the presence antibodies against paramyxoviruses among various bat species in India, Italy, China, Vietnam, Indonesia and many African countries, thereby suggesting bats as reservoir hosts for the virus (Sasaki *et al*., 2012; Yuan *et al*., 2014; Yadav *et al*., 2016; Rizzo *et al*., 2017; Berto *et al*., 2018; Markotter *et al*., 2019).

Coronaviridae

Before the outbreak of severe acute respiratory syndrome (SARS), coronaviruses were known to cause mild respiratory and enteric illnesses in humans and animals. In 2002, SARS emerged in Guangdong province in China, lasted for 8 months and claimed 774 lives out of 8096 patients in 29 countries (WHO, 2004). Initially, Himalaysan palm civets were suggested to be the most likely host responsible for human transmission (Tu *et al*., 2004; Kan *et al*., 2005), however, the role of bats as the reservoir hosts was later established when 92% similarity was demonstrated between human SARS-CoV and SARS-like CoV in horseshoe bats (*Rhinolophus* spp.) (Lau *et al*., 2005; Li *et al*., 2005). Subsequently, many coronaviruses that were phylogenetically related to SARS-CoV were discovered in bats species of Asian, European and African countries (Cui *et al*., 2019), predicting the origin of SARS-CoV from bat coronaviruses (Hu *et al*., 2017).

A decade later in 2012, Middle East Respiratory Syndrome emerged in Saudi Arabia which caused severe respiratory illness in humans in close contact with infected dromedary camels or camel products (Azhar *et al*., 2014; Conzade *et al*., 2018). Seroprevalence of MERS-CoV in dromedary camels of the Arabian peninsula and North Africa established the role of camels as the natural reservoirs (Hemida *et al*., 2013; Corman *et al*., 2014; Haagmans *et al*., 2014; Müller *et al*., 2014; Falzarano *et al*., 2017). However, subsequent studies followed, which established strong evidence of bats being the ancestral hosts of the virus (Memish *et al*., 2013; Anthony *et al*., 2017; Widagdo *et al*., 2017). Limited human to human transmission was observed in nosocomial settings (Oboho *et al*., 2015). Till now, MERS-CoV has claimed more than 850 lives out of 2494 diseased with a case fatality rate of 35% (Al-Dorzi *et al*., 2016).

The most recent outbreak of a novel coronavirus SARS-CoV-2 started from Wuhan in China in 2019 and spread all over the globe. Index cases were associated with the wet markets in Wuhan city, but the role of any intermediate host in transmission to humans is unknown yet. Genome analysis of SARS-CoV 2 found 91% similarity to Pangolin coronavirus (Lam *et al*., 2020) and more than 96% similarity to Bat coronavirus (Lam *et al*., 2020), suggesting bats as the possible primary reservoir. The virus is characterized by a low mortality rate (2-3%) yet high infectivity and rapid human to human transmission aided by global travel. A study revealed the presence of pathogenic coronaviruses, capable of recombination in *Rousettus* and *Pteropus* species of bats from different states of India (Yadav *et al*., 2020).

Public health measures

To enhance the capacity for control and mitigation of the emergence of bat-borne disease outbreaks, a deeper understanding of host-virus dynamics is of utmost

Table 1: Events of outbreaks of a few Zoonoses with the case fatality rate.					
Virus	Year	Country	Cases	Deaths	Case fatality rate
Marburg	1967	Germany	29	$\overline{7}$	24%
	1975	South Africa	3	1	33%
	1975	South Africa	3	1	33%
	1987	Kenya	1	1	100%
	1998 to 2000	Democratic Republic of the Congo	154	128	83%
	2005	Angola	374	329	88%
	2007	Uganda	4	$\overline{2}$	50%
	2008	United States of America (ex-Uganda)	1	0	0%
	2008	Netherland (ex-Uganda)	1	1	100%
	2012	Uganda	15	4	27%
	2014	Uganda	1	1	100%
	2017	Uganda	3	3	100%
Ebola	1976	Democratic Republic of the Congo	318	280	88%
	1977	Democratic Republic of the Congo	1	$\mathbf{1}$	100%
	1995	Democratic Republic of the Congo	315	254	81%
	2014-2016	Sierra Leone	14124	3956	28%
	2014-2016	Liberia	10675	4809	45%
	2014-2016	Guinea	3811	2543	67%
	2018-2020	Democratic Republic of the Congo	3481	2299	66%
	2021	Guinea	Ongoing	$\overline{}$	$\overline{}$
	2021	Democratic Republic of the Congo	Ongoing	$\overline{}$	\blacksquare
Hendra	1994	Mackay, Queensland	1	1	100%
	1994	Hendra Queensland	2	1	50%
	2004	Gordonvale, Cairns, Queensland	1	1	100%
	2008	Redlands, Queensland	2	1	50%
Nipah	1998-1999	Malaysia	265	105	40%
	2001	Siliguri	66		75%
	2001	Bangladesh	13	9	69%
	2003	Bangladesh	12	8	67%
	2004	Bangladesh	42	14	33%
	2004	Bangladesh	36	27	75%
	2005	Bangladesh	12	11	92%
	2007	India	50	5	10%
	2008	Bangladesh	9	8	88%
	2010	Bangladesh	8	7	87.5%
	2011	Bangladesh		21	
	2018	India		21	
	2019	India		0	0%
	2021	India	1	1	100%
SARS	2002	Guangdong province of China	7429	685	9.2%
	2003	US	27	$\mathbf 0$	0%
MERS	2012-2014	Saudi Arabia	688	282	41%
	2014	US	\overline{c}	0	0%
	2014	Netherlands	1	$\mathbf 0$	0%
	2015	South Korea	184	19	10.3%
	2015	Philippines	\overline{c}	0	0%
	2015	United Kingdom	2	0	0%
	2018	South Korea	1	0	0%
	2019	Saudi Arabia	14	5	35.7%

Bat's Role in Emergence and Spillover of Viral Zoonotic Diseases: A Review

(All outbreak events from centre for disease control and prevention).

importance. Insights regarding the ecology of bats and viruses along with the ecological and socio-economic factors triggering the outbreaks are the keystones for drafting effective control strategies. Intervention at each level of disease transmission cycle must be designed, for instance, conservation and restoration of bats by providing habitat along with ample food supply in forests would reduce the stress and consequently curb viral shedding occasions. Similarly, by reducing or delaying the contact between reservoir host and susceptible population would undermine the viral survival in the environment. Besides, steps to modify the host susceptibility by vaccination would hamper effective disease transmission and outbreaks. Strategies such as modification of landscaping and agricultural practices around wildlife habitat must be controlled to reduce the contact between humans, livestock and wild animals. Vigilance towards the movement of animals for research purposes, meat production, or breeding purposes must be enhanced with screening by agencies at multiple levels in the supply channel. Strict laws must be formulated to cease the hunting and illegal trade of wild animals and must be rigorously implemented. Once formulated, the control strategies and the risk about the outbreak must be effectively communicated with the general public and experts such as physicians, veterinarians and administrators. Most importantly, improved surveillance of bats and their ecology at the international level to cover nearly all geographical locations coordinated with zoonoses and disease research communities is the pressing priority. There is a dearth of ecological as well as pathogen research on bats in India. A total of only 61 bat articles could be found on PubMed from India, amongst them the first article was published in the year 1965. Out of a total 61, only 28 articles were dedicated to pathogen research of which 17 articles have been published in the past 10 years. There is an urgent need to enhance the ecological and pathogen research in bats in India to understand the host-pathogen dynamics. A holistic approach must be adopted for identification of the bat population in the area, detection of potential zoonotic pathogens they harbour and the ability of the viruses to recombine. An integrated approach must be adopted for unravelling the host-virus dynamics as well as providing mutually beneficial solutions for bat conservation and safeguarding animal and public health at a global level.

CONCLUSION

Bats have been discovered to host a wide range of zoonotic infections, including some of the most virulent RNA viruses capable of crossing species barriers and infecting humans, livestock and other animals. It is evident that a number of anthropogenic causes, including urbanization, traffic in animals and deforestation, have had a significant impact on the origin and reemergence of zoonotic illnesses. Understanding the ecology of bats and viruses, as well as the environmental and socioeconomic elements that contribute to outbreaks, is crucial for developing successful control strategies. It is essential to implement interventions at each stage of the disease transmission cycle, such as preserving and restoring bat habitats and ensuring an adequate food supply, in order to reduce stress and virus shedding. This emphasizes the necessity for an integrated strategy to understand host-virus dynamics, safeguard animal and public health and conserve bat populations.

Conflict of interest: None.

REFERENCES

- Ahn, M. anderson, D.E., Zhang, Q., Tan, C.W., Lim, B.L., Luko K., Wen, M., Chia, W.N., Mani, S., Wang, L.C. and Ng, J.H. (2019). Dampened NLRP3-mediated inflammation in bats and implications for a special viral reservoir host. Nature Microbiology. 4: 789-99.
- Al-Dorzi, H.M., Van, K.M.D., Peiris, J.M. and Arabi, Y.M. (2016). Middle east respiratory syndrome coronavirus. ERS. Monograph. 9781849840705: 21-34.
- Alexander, K.A., Sanderson, C.E., Marathe, M., Lewis, B.L., Rivers, C.M., Shaman, J., Drake, J.M., Lofgren, E., Dato, V.M., Eisenberg, M.C. and Eubank, S. (2015). What factors might have led to the emergence of Ebola in West Africa? PLoS. Neglected Tropical Diseases. 9: e0003652.
- Altizer, S., Dobson, A., Hosseini, P., Hudson, P., Pascual, M. and Rohani, P. (2006). Seasonality and the dynamics of infectious diseases. Ecology Letters. 9: 467-84.
- Amman, B.R., Carroll, S.A., Reed, Z.D, Sealy, T.K., Balinandi, S., Swanepoel, R., Kemp, A., Erickson, B.R., Comer, J.A., Campbell, S. and Cannon, D.L. (2012). Seasonal pulses of Marburg virus circulation in juvenile *Rousettus aegyptiacus* bats coincide with periods of increased risk of human infection. PLoS. Pathogens. 8: e1002877.
- Anthony, S.J., Gilardi, K., Menachery, V.D, Goldstein, T., Ssebide B., Mbabazi, R., Navarrete-Macias, I., Liang, E., Wells, H., Hicks, A. and Petrosov, A. (2017). Further evidence for bats as the evolutionary source of middle East respiratory syndrome coronavirus. M Bio. 8(2): e00373-17.
- Azhar, E.I., El-Kafrawy, S.A., Farraj, S.A., Hassan, A.M., Al-Saeed, M.S., Hashem, A.M. and Madani, T.A. (2014). Evidence for camel-to-human transmission of MERS. coronavirus. New England Journal of Medicine. 370: 2499-505.
- Badrane, H., Bahloul, C., Perrin, P. and Tordo, N. (2001). Evidence of two Lyssavirus phylogroups with distinct pathogenicity and immunogenicity. Journal of Virology. 75: 3268-76.
- Baer, G.M. (2017). The natural history of rabies. Routledge. 640. https://doi.org/10.1201/9780203736371.
- Banerjee, A., Baker, M.L., Kulcsar, K., Misra, V., Plowright, R. and Mossman, K. (2020). Novel insights into immune systems of bats. Frontiers in Immunology. 11: 26. https://doi.org/ 10.3389/fimmu.2020.00026.
- Banyard, A.C., Evans, J.S., Luo, T.R. and Fooks, A.R. (2014). Lyssaviruses and bats: Emergence and zoonotic threat. Viruses. 6: 2974-90.
- Beena, V. and Saikumar, G. (2019). Emerging horizon for bat borne viral zoonoses. Virus Disease. 30: 321-8.
- Berto, A., Anh, P.H., Carrique Mas, J.J., Simmonds, P., Cuong, N.V., Tue, N.T., Dung, N.V., Woolhouse, M.E., Smith, I., Marsh, G.A. and Bryant, J.E. (2018). Detection of potentially novel paramyxovirus and coronavirus viral RNA in bats and rats in the Mekong Delta region of southern Viet Nam. Zoonoses and Public Health. 65: 30-42.
- Brauburger, K., Hume, A.J., Mühlberger, E. and Olejnik, J. (2012). Forty-five years of Marburg virus research. Viruses. 4: 1878-927.
- Brook, C.E., Boots, M., Chandran, K., Dobson, A.P., Drosten, C., Graham, A.L., Grenfell, B.T., Müller, M.A., Ng, M., Wang, L.F. and van Leeuwen A. (2020). Accelerated viral dynamics in bat cell lines, with implications for zoonotic emergence. Elife. 9: e48401.
- Brook, Cara, E. and Dobson, A.P. (2015). Bats as 'special' Reservoirs for emerging zoonotic pathogens. Trends in Microbiology. 23: 172-80.
- Calisher, C.H., Childs, J.E., Field, H.E., Holmes, K.V. and Schountz, T. (2006). Bats: Important reservoir hosts of emerging viruses.Clinical Microbiology Reviews. 19: 531-45.
- Chen, L., Liu, B., Yang, J. and Jin, Q. (2014). DBatVir: The Database of Bat-Associated Viruses. Database, bau021.
- Chua, K.B., Goh, K.J., Wong, K.T., Kamarulzaman, A., Tan, P.S., Ksiazek, T., Zaki, S.R., Paul, G., Lam, S.K. and Tan, C.T. (1999). Fatal encephalitis due to Nipah virus among pigfarmers in Malaysia. Lancet. 354: 1257-9.
- Chua, K.B., Koh, C.L., Hooi, P.S., Wee, K.F., Khong, J.H., Chua, B.H., Chan, Y.P., Lim, M.E. and Lam, S.K. (2002).Isolation of Nipah virus from Malaysian Island flying-foxes. Microbes and Infection. 4: 145-51.
- Chua, K.B. (2000). Nipah virus: A. recently emergent deadly paramyxovirus. Science. 288(5470): 1432-5.
- Conrad, J.L., Isaacson, M., Smith, E.B., Wulff, H., Crees, M., Geldenhuys, P. and Johnston, J. (1978). Epidemiologic investigation of Marburg virus disease, Southern Africa. The American Journal of Tropical Medicine and Hygiene. 27: 1210-5.
- Conzade, R., Grant, R., Malik, M.R., Elkholy, A., Elhakim, M., Samhouri, D., Embarek, P.K.B. and Kerkhove, M.D.V. (2018). Reported direct and indirect contact with dromedary camels among laboratory-confirmed MERS-CoV. Cases. Viruses. 10: 425. doi: 10.3390/v10080425.
- Corman, V.M., Jores, J., Meyer, B., Younan, M., Liljander, A., Said, M.Y., Gluecks, I., Lattwein, E., Bosch, B.J., Drexler, J.F., Bornstein, S., Drosten, C. and Müller, M.A. (2014). Antibodies against MERS. coronavirus in dromedary camels, Kenya, 1992-(2013. Emerging Infectious Diseases. 20: 1319-22.
- Cui, J., Li, F. and Shi, Z.L. (2019). Origin and evolution of pathogenic coronaviruses. Nature Reviews Microbiology. 17: 181-192.
- Daszak, P., Cunningham, A.A. and Hyatt, A.D. (2000). Emerging infectious diseases of wildlife-threats to biodiversity and human health. Science. 287: 443-9.
- Dovih, P., Laing, E.D, Chen, Y., Low, D.H.W., Ansil, B.R., Yang, X., Shi, Z., Broder, C.C., Smith, G. J.D., Linster, M., Ramakrishnan, U. and Mendenhall, I.H. (2019). Filovirus-reactive antibodies in humans and bats in Northeast India imply zoonotic spillover. PLoS. Neglected Tropical Diseases. 13:e0007733.
- Drexler, J.F., Corman, V.M., Wegner, T., Tateno, A.F., Zerbinati, R.M., Gloza-Rausch, F., Seebens, A., Müller, M.A. and Drosten, C. (2011). Amplification of emerging viruses in a bat colony. Emerging Infectious Diseases. 17: 449-56.
- Epstein, J.H., Prakash, V., Smith, C.S., Daszak, P., McLaughlin, A.B., Meehan, G., Field, H.E. and Cunningham, A.A. (2008). Henipavirus infection in fruit bats (*Pteropus giganteus*), India. Emerging Infectious Diseases. 14: 1309-11.
- Falzarano, D., Kamissoko, B., de Wit, E., Maïga, O., Cronin, J., Samaké, K., Traoré, A., Milne-Price, S., Munster, V.J., Sogoba, N., Niang, M., Safronetz, D. and Feldmann, H. (2017). Dromedary camels in Northern Mali have high seropositivity to MERS-CoV. One Health. 3: 41-43.
- Fenton, M.B. (2010). Convergences in the diversification of bats. Current Zoology. 56: 454-68.
- Field, H. and Kung, N. (2011). Henipaviruses-unanswered questions of lethal zoonoses. Current Opinion in Virology. 1: 658-61.
- Field, H., Young, P., Yob, J.M., Mills, J., Hall, L. and Mackenzie, J. (2001). The natural history of Hendra and Nipah viruses. Microbes and Infection. 3: 307-14.
- Fleming, T.H. (2010). Bat migration. Encyclopedia of Animal Behavior. 145-149.
- George, D.B., Webb, C.T., Farnsworth, M.L., O'Shea, T.J., Bowen, R.A., Smith, D.L., Stanley, T.R., Ellison, L.E. and Rupprecht, C.E. (2011). Host and viral ecology determine bat rabies seasonality and maintenance. Proceedings of the National Academy of Sciences of the United States of America. 108: 10208-13.
- Gerow, C.M., Rapin, N., Voordouw, M.J., Elliot, M., Misra, V. and Subudhi, S. (2019). Arousal from hibernation and reactivation of Eptesicus fuscus gammaherpesvirus (EfHV) in big brown bats. Transboundary and Emerging Diseases. 66: 1054-1062.
- Giles, J.R., Eby, P., Parry, H., Peel, A.J., Plowright, R.K., Westcott, D.A. and McCallum, H. (2018). Environmental drivers of spatiotemporal foraging intensity in fruit bats and implications for Hendra virus ecology. Scientific Reports. 22; 8: 9555.
- Greenhall, A.M. and Denny, G.C. (2018). Transmission of Pathogenic Microorganisms by Vampire Bats. In Book: Natural History of Vampire Bats. 167-189.
- Haagmans, B.L., Dhahiry, S.H.A., Reusken, C.B., Raj, V.S., Galiano, M., Myers, R., Godeke, G.J., Jonges, M. *et al*. (2014). Middle East respiratory syndrome coronavirus in dromedary camels: An outbreak investigation. The Lancet Infectious Diseases. 14: 140-5.
- Harris, S.L., Brookes, S.M., Jones, G., Hutson, A.M., Racey, P.A., Aegerter, J., Smith, G.C., McElhinney, L.M. and Fooks, A.R. (2006). European bat lyssaviruses: Distribution, prevalence and implications for conservation. Biological Conservation. 131: 193-210.
- Hayman, D.T., Bowen, R.A., Cryan, P.M., McCracken, G.F., O'Shea, T.J., Peel, A.J., Gilbert, A., Webb, C.T. and Wood, J.L. (2013). Ecology of zoonotic infectious diseases in bats: Current knowledge and future directions. Zoonoses and Public Health. 60: 2-21.
- Hayman, D.T., Emmerich, P., Yu, M., Wang, L.F., Suu-Ire, R., Fooks, A.R., Cunningham, A.A. and Wood, J.L. (2010). Longterm survival of an urban fruit bat seropositive for Ebola and Lagos bat viruses. PLoS. One. 5: e11978.
- Hayman, D.T., Yu, M., Crameri, G., Wang, L.F., Suu-Ire, R., Wood, J.L. and Cunningham, A.A. (2012). Ebola virus antibodies in fruit bats, Ghana, West Africa. Emerging Infectious Diseases. 18: 1207-9.
- Hegde, S.T., Sazzad, H.M., Hossain, M.J., Alam, M.U., Kenah, E., Daszak, P., Rollin, P., Rahman, M., Luby, S.P. and Gurley, E.S. (2016). Investigating rare risk factors for nipah virus in Bangladesh: 2001-2012. Ecohealth. 13: 720-728.
- Hemida, M.G., Perera, R.A., Wang, P., Alhammadi, M.A., Siu, L., Li, M., Poon, L.L., Saif, L., Alnaeem, A. and Peiris, M. (2013). Middle East respiratory syndrome (MERS) coronavirus seroprevalence in domestic livestock in Saudi Arabia, 2010 to 2013. Eurosurveillance. 18: 20659.
- Herriman, R. (2019). Nipah Virus Reported in Thakurgaon, Bangladesh. Outbreak News Today. http://outbreaknewstoday.com/ nipah-virus-reported-thakurgaon-bangladesh-85881/.
- Hu, B., Zeng, L.P., Yang, X.L., Ge, X.Y., Zhang, W., Li, B., Xie, J.Z., Shen, X.R., Zhang, Y.Z. *et al*. (2017). Discovery of a rich gene pool of bat SARS-related coronaviruses provides new insights into the origin of SARS. coronavirus. PLoS. Pathogens. 13: e1006698.
- Jayme, S.I., Field, H.E., de Jong, C., Olival, K.J., Marsh, G., Tagtag, A.M., Hughes, T., Bucad, A.C., Barr, J. *et al*. (2015). Molecular evidence of Ebola Reston virus infection in Philippine bats. Virology Journal. 12:107. doi: 10.1186/ s12985-015-0331-3.
- Johnson, E.D., Johnson, B.K., Silverstein, D., Tukei, P., Geisbert, T.W., Sanchez, A.N. and Jahrling, P.B. (1996). Characterization of a new Marburg virus isolated from a 1987 fatal case in Kenya. Archives of Virology, Supplement. 11: 101-14.
- Jones, K.E., Bininda-Emonds, O.R.P. and Gittleman, J.L. (2005). Bats, clocks and rocks: Diversification patterns in chiroptera. Evolution. 59: 2243-2255.
- Jones, K.E., Patel, N.G., Levy, M.A., Storeygard, A., Balk, D., Gittleman, J.L. and Daszak, P. (2008). Global trends in emerging infectious diseases. Nature. 451: 990-3.
- Kan, B., Wang, M., Jing, H., Xu, H., Jiang, X., Yan, M., Liang, W., Zheng, H., Wan, K., Liu, Q. *et al*. (2005). Molecular evolution analysis and geographic investigation of severe acute respiratory syndrome coronavirus-like virus in palm civets at an animal market and on farms. Journal of Virology. 79: 11892-900.
- Lam, T.T., Jia, N., Zhang, Y.W., Shum, M.H., Jiang, J.F., Zhu, H.C., Tong, Y.G., Shi, Y.X., Ni, X.B. *et al*. (2020). Identifying SARS-CoV-2-related coronaviruses in Malayan pangolins. Nature. 583: 282-285.
- Lau, S.K., Woo, P.C., Li, K.S., Huang, Y., Tsoi, H.W., Wong, B.H., Wong, S.S., Leung, S.Y., Chan, K.H. and Yuen, K.Y. (2005). Severe acute respiratory syndrome coronaviruslike virus in Chinese horseshoe bats. Proceedings of the National Academy of Sciences of the United States of America. 102: 14040-5.
- Lee, B.P.Y.H., Struebig, M.J., Rossiter, S.J. and Kingston, T. (2015). ncreasing Concern over Trade in Bat Souvenirs from South-East Asia. Oryx. 49: 204. doi: 10.3389/fvets.2021. 651304.
- Leroy, E.M., Epelboin, A., Mondonge, V., Pourrut, X., Gonzalez, J.P., Muyembe-Tamfum, J.J. and Formenty, P. (2009). Human Ebola outbreak resulting from direct exposure to fruit bats in Luebo, Democratic Republic of Congo. (2007). Vector-Borne and Zoonotic Diseases. 9: 723-8.
- Leroy, E.M., Kumulungui, B., Pourrut, X., Rouquet, P., Hassanin, A., Yaba, P., Délicat, A., Paweska, J.T., Gonzalez, J.P. and Swanepoel, R. (2005). Fruit bats as reservoirs of Ebola virus. Nature. 438: 575-6.
- Li, Q., Guan, X., Wu, P., Wang, X., Zhou, L., Tong, Y., Ren, R., Leung, K.S.M., Lau, E.H.Y., Wong, J.Y. *et al*. (2020). Early transmission dynamics in Wuhan, China, of novel Coronavirusinfected pneumonia. New England Journal of Medicine. 382: 1199-1207.
- Li, W., Shi, Z., Yu, M., Ren, W., Smith, C., Epstein, J.H., Wang, H., Crameri, G., Hu, Z., Zhang, H. *et al*. (2005). Bats are natural reservoirs of SARS-like coronaviruses. Science. 310: 676-9.
- Looi, L.M. and Chua, K.B. (2007). Lessons from the Nipah virus outbreak in Malaysia. The Malaysian Journal of Pathology. 29: 63-7.
- Luby, S.P., Rahman, M., Hossain, M.J., Blum, L.S., Husain, M.M., Gurley, E., Khan, R., Ahmed, B. N. *et al*. (2006). Foodborne transmission of Nipah virus, Bangladesh. Emerging Infectious Diseases. 12: 1888-94.
- Mani, R.S., Dovih, D.P., Ashwini, M.A., Chattopadhyay, B., Harsha, P.K., Garg, K.M., Sudarshan, S., Puttaswamaiah, R., Ramakrishnan, U. and Madhusudana, S.N. (2017). Serological evidence of lyssavirus infection among bats in Nagaland, a North-Eastern state in India. Epidemiology and Infection. 145: 1635-1641.
- Markotter, W., Geldenhuys, M., Jansen van Vuren, P., Kemp, A., Mortlock, M., Mudakikwa, A., Nel, L., Nziza, J., Paweska, J. and Weyer, J. (2019). Paramyxo-and Coronaviruses in Rwandan bats. Tropical Medicine and Infectious Disease. 4: 99. doi: 10.3390/tropicalmed4030099.
- Memish, Z.A., Mishra, N., Olival, K.J., Fagbo, S.F., Kapoor, V., Epstein, J.H., Alhakeem, R. *et al*. (2013). Middle East respiratory syndrome coronavirus in bats, Saudi Arabia. Emerging Infectious Diseases. 19: 1819-23.
- Meredith, C.D., Prossouw, A.P. and Koch, H.V. (1971). An unusual case of human rabies thought to be of chiropteran origin. South African Medical Journal. 45: 767-9.
- Mildenstein, T., Tanshi, I. and Racey, P.A. (2016). Bats in the Anthropocene: Conservation of bats in a changing world. Exploitation of Bats for Bushmeat and Medicine. 325-75.
- Moratelli, R. and Calisher, C.H. (2015). Bats and zoonotic viruses: Can we confidently link bats with emerging deadly viruses? Memorias Do Instituto Oswaldo Cruz. 110: 1-22.
- Müller, M.A., Corman, V.M., Jores, J., Meyer, B., Younan, M., Liljander, A., Bosch, B.J., Lattwein, E., Hilali, M., Musa, B.E., Bornstein, S. and Drosten, C. (2014). MERS. coronavirus neutralizing antibodies in camels, Eastern Africa, 1983- 1997. Emerging Infectious Diseases. 20: 2093-5.
- Murray, K., Selleck, P., Hooper, P., Hyatt, A., Gould, A., Gleeson, L., Westbury, H., Hiley, L., Selvey, L., Rodwell, B. and Ketterer, P. (1995). A morbillivirus that caused fatal disease in horses and humans. Science. 268: 94-7.
- Nel, L.H. and Rupprecht, C.E. (2007). Emergence of lyssaviruses in the Old World: The case of Africa. Current Topics in Microbiology and Immunology. 315: 161-93.
- Oboho, I.K., Tomczyk, S.M., Al-Asmari, A.M., Banjar, A.A., Al-Mugti, H., Aloraini, M.S., Alkhaldi, K.Z., Almohammadi, E.L., Alraddadi, B.M., Gerber, S.I., Swerdlow, D.L., Watson, J.T. and Madani, T.A. (2015). 2014 MERS-CoV. outbreak in Jeddah-a link to health care facilities. New England Journal of Medicine. 372: 846-54.
- Olival, K.J., Islam, A., Yu, M., Anthony, S.J., Epstein, J.H., Khan, S.A., Khan, S.U., Crameri, G., Wang, L.F., Lipkin, W.I., Luby, S.P. and Daszak, P. (2013). Ebola virus antibodies in fruit bats, Bangladesh. Emerging Infectious Diseases. 19: 270-3.
- O'Shea, T.J., Cryan, P.M., Cunningham, A.A., Fooks, A.R., Hayman, D.T., Luis, A.D., Peel, A.J., Plowright, R.K. and Wood, J.L. (2014). Bat flight and zoonotic viruses. Emerging Infectious Diseases. 20: 741-5.
- Paweska, J.T., Jansen van Vuren, P., Fenton, K.A., Graves, K., Grobbelaar, A.A., Moolla, N., Leman, P., Weyer, J., Storm, N., McCulloch, S.D. *et al*. (2015). Lack of Marburg virus transmission from experimentally infected to susceptible in-contact Egyptian fruit bats. Journal of Infectious Diseases. 212: S109-S118.
- Plowright, R.K., Becker, D.J., Crowley, D.E., Washburne, A.D., Huang, T., Nameer, P.O., Gurley, E. S. and Han, B.A. (2019). Prioritizing surveillance of Nipah virus in India. PLoS. Neglected Tropical Diseases. 13: e0007393.
- Plowright, R.K., Foley, P., Field, H.E., Dobson, A.P., Foley, J.E., Eby, P. and Daszak, P. (2011). Urban habituation, ecological connectivity and epidemic dampening: the emergence of Hendra virus from flying foxes (*Pteropus* spp.). Proceedings of the Royal Society B: Biological Sciences. 278: 3703-12.
- Pourrut, X., Souris, M., Towner, J.S., Rollin, P.E., Nichol, S.T., Gonzalez, J.P. and Leroy, E. (2009). Large serological survey showing co-circulation of Ebola and Marburg viruses in Gabonese bat populations and a high seroprevalence of both viruses in *Rousettus aegyptiacus*. BMC Infectious Diseases. 9: 159. https://doi.org/10.1186/1471-2334-9- 159.
- Rizzo, F., Edenborough, K.M., Toffoli, R., Culasso, P., Zoppi, S., Dondo, A., Robetto, S., Rosati, S., Lander, A., Kurth, A., Orusa, R., Bertolotti, L. and Mandola, M.L. (2017). Coronavirus and paramyxovirus in bats from Northwest Italy. BMC Veterinary Research. 13: 396. doi: 10.1186/ s12917-017-1307-x.
- Shope, R.E., Murphy, F.A., Harrison, A.K., Causey, O.R., Kemp, G.E., Simpson, D.I.H. and Moore, D.L. (1970). Two African viruses serologically and morphologically related to rabies virus. Journal of Virology. 6: 690-692.
- Sasaki, M., Setiyono, A., Handharyani, E., Rahmadani, I., Taha, S., Adiani, S., Subangkit, M., Sawa, H., Nakamura, I. and Kimura, T. (2012). Molecular detection of a novel paramyxovirus in fruit bats from Indonesia. Virology Journal. 9: 240. doi: 10.1186/1743-422X-9-240.
- Schmid, R. (1993). Mammal species of the world: A taxonomic and geographic reference. JSTOR. 512-512.
- Schneider, M.C., Romijn, P.C., Uieda, W., Tamayo, H., da Silva, D.F., Belotto, A., da Silva, J.B. and Leanes, L.F. (2009). Rabies transmitted by vampire bats to humans: an emerging zoonotic disease in Latin America? Revista Panamericana de Salud Publica/Pan American Journal of Public Health. 25: 260-9.
- Seltmann, A., Corman, V.M., Rasche, A., Drosten, C., Czirják, G.Á., Bernard, H., Struebig, M.J. and Voigt, C.C. (2017). Seasonal fluctuations of astrovirus, but not coronavirus shedding in bats inhabiting human-modified tropical forests. Eco Health. 14: 272-84.
- Timen, A., Koopmans, M.P., Vossen, A.C, van Doornum, G.J., Günther, S., van den Berkmortel, F., Verduin, K.M., Dittrich, S., Emmerich, P., Osterhaus, A.D., van Dissel, J.T. and Coutinho, R. A. (2009). Response to imported case of Marburg hemorrhagic fever, the Netherland. Emerging Infectious Diseases. 15: 1171-5.
- Towner, J.S., Amman, B.R., Sealy, T.K., Carroll, S.A., Comer, J.A., Kemp, A., Swanepoel, R., Paddock, C.D. *et al*. (2009). Isolation of genetically diverse Marburg viruses from Egyptian fruit bats. PLoS. Pathogens. 5: e1000536.
- Tu, C., Crameri, G., Kong, X., Chen, J., Sun, Y., Yu, M., Xiang, H., Xia, X., Liu, S., Ren, T., Yu, Y. *et al*. (2004). Antibodies to SARS. coronavirus in civets. Emerging Infectious Diseases. 10: 2244-8.
- Turmelle, A.S., Allen, L.C., Jackson, F.R., Kunz, T.H., Rupprecht, C.E. and McCracken, G.F. (2010). Ecology of rabies virus exposure in colonies of Brazilian free-tailed bats (*Tadarida brasiliensis*) at natural and man-made roosts in Texas. Vector-Borne and Zoonotic Diseases. 10(2): 165-75.
- WHO, (2004). Summary of probable SARS. cases with onset of illness from 1 November (2002 to 31 July 2003 (Based on data as of the 31 December 2003.). World Health Organization , Global Alert and Response (GAR).
- Widagdo, W., Begeman, L., Schipper, D., Run, P.R.V., Cunningham, A.A., Kley, N., Reusken, C.B., Haagmans, B.L. and van den Brand, J.M.A. (2017). Tissue distribution of the MERS-coronavirus receptor in bats. Scientific Reports. 7: 1193.
- Wilkinson, G.S. and South, J.M. (2002). Life history, ecology and longevity in bats. Aging Cell. 1: 124-31.
- Woolhouse, M. and Gaunt, E. (2007). Ecological origins of novel human pathogens. Critical Reviews in Microbiology. 33: 231-42.
- Yadav, P.D., Raut, C.G., Shete, A.M., Mishra, A.C., Towner, J.S., Nichol, S.T. and Mourya, D.T. (2012). Detection of Nipah virus RNA in fruit bat (*Pteropus giganteus*) from India. American Journal of Tropical Medicine and Hygiene. 87: 576-8.
- Yadav, P.D., Shete, A.M., Kumar, G.A., Sarkale, P., Sahay, R.R., Radhakrishnan, C., Lakra, R., Pardeshi, P., Gupta, N. *et al*. (2019). Nipah virus sequences from humans and bats during Nipah Outbreak, Kerala, India, 2018. Emerging Infectious Diseases. 25: 1003-1006.
- Yadav, P.D., Shete-Aich, A., Nyayanit, D.A., Pardeshi, P., Majumdar, T., Balasubramanian, R., Ullas, P.T., Mohandas, S. *et al*. (2020). Detection of coronaviruses in *Pteropus* and *Rousettus* species of bats from different States of India. Indian Journal of Medical Research. 151: 226-235.
- Yadav, P., Sarkale, P., Patil, D., Shete, A., Kokate, P., Kumar, V., Jain, R., Jadhav, S., Basu, A., Pawar, S., Sudeep, A., Gokhale, M., Lakra, R. and Mourya, D. (2016). Isolation of Tioman virus from *Pteropus giganteus* bat in North-East region of India. Infection, Genetics and Evolution. 45: 224-229.
- Yob, J.M., Field, H., Rashdi, A.M., Morrissy, C., van der Heide, B., Rota, P., bin Adzhar, A., White, J., Daniels, P., Jamaluddin, A. and Ksiazek, T. (2001). Nipah virus infection in bats (order Chiroptera) in peninsular Malaysia. Emerging Infectious Diseases. 7: 439-41.
- Young, P.L., Halpin, K., Selleck, P.W., Field, H., Gravel, J.L., Kelly, M.A. and Mackenzie, J.S. (1996). Serologic evidence for the presence in *Pteropus* bats of a paramyxovirus related to equine morbillivirus. Emerging Infectious Diseases. 2: 239-40.
- Yuan, J., Zhang, Y., Li, J., Zhang, Y., Wang, L.F. and Shi, Z. (2012). Serological evidence of ebolavirus infection in bats, China. Virology Journal. 9: 236. doi.org/10.1186/1743- 422X-9-236.
- Yuan, L., Li, M., Li, L., Monagin, C., Chmura, A.A., Schneider, B.S., Epstein, J.H., Mei, X., Shi, Z., Daszak, P. and Chen, J. (2014). Evidence for retrovirus and paramyxovirus infection of multiple bat species in china. Viruses. 6: 2138-54.
- Zhou, P., Yang, X. L., Wang, X. G., Hu, B., Zhang, L., Zhang, W., Si, H. R., Zhu, Y., Li, B., Huang, C.L. *et al*. (2020). A pneumonia outbreak associated with a new coronavirus of probable bat origin. Nature. 579: 270-273.