

# Bats and viruses or how to live together in harmony

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*Bats have long been ignored or even despised, and in recent years they have been the subject of increasing public and research attention. Endowed with exceptional abilities such as flight and echolocation, bats intrigue the former. Their unexpected longevity given their size and, above all, a unique immune system that enables them to tolerate many viruses that are poorly tolerated by terrestrial mammals, make them excellent study models for the latter. However, this improved image is tarnished by the knowledge of their links with pathogenic viruses. Indeed, bats seem to play a crucial role in the emerging virus epidemics that have been shaking the world population with increasing frequency in recent years. The current COVID-19 pandemic is no exception, and has once again brought bats to the forefront. This raises many questions: How are bats preferred hosts for pathogenic viruses? What role did they play in the origin of the COVID-19 pandemic? Are they indeed responsible for the emergence of the new viral diseases that are increasingly affecting humans and domestic animals?*

## 1. Bats in the spotlight

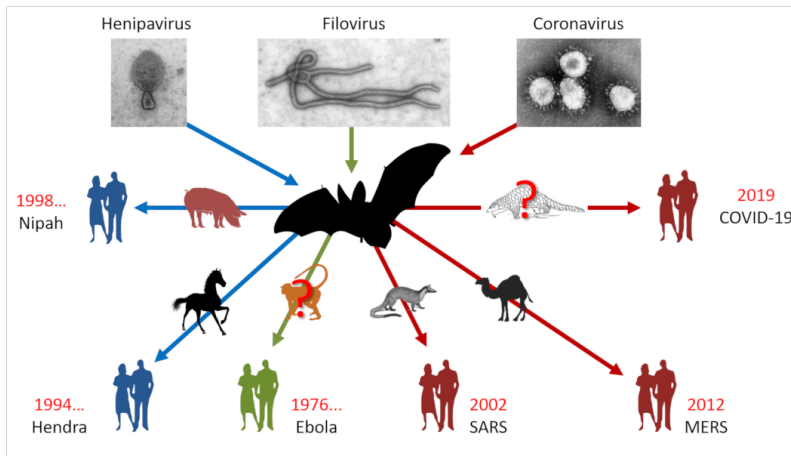


Figure 1. Bats are the natural hosts of many emerging viruses responsible for epidemics. [Sources: Henipavirus, CSIRO, CC BY 3.0, via Wikimedia Commons / Filovirus, Photo Credit : CDC/ Cynthia Goldsmith, Public domain, via Wikimedia Commons / Coronavirus, public domain]

The beginning of 2020 was marked by the emergence of a respiratory disease that rapidly spread among the world's population to such an extent that it had to be recognized that humans were facing, after the relatively limited influenza A pandemic in 2009-2010, the **first major pandemic** of the 21<sup>st</sup> century (See [Viral Pandemics of the Modern Era](#)). It turns out that the pathogen responsible for this pandemic is a coronavirus, similar to the one that caused an epidemic of respiratory infections mainly localized in China in 2002-2003. The latter was then called *severe acute respiratory syndrome coronavirus* or SARS-CoV. It has recently been renamed SARS-CoV-1 to differentiate it from the new SARS-CoV-2, which is responsible for the disease named by the World Health Organization (WHO) COVID-19 for **CO**rona**VI**rus **D**isease **2019**.

As with SARS-CoV-1, bats appear to be involved in the viral transmission chain. Indeed, preliminary results have shown that SARS-CoV-2 is thought to result from the recombination of a bat coronavirus [1] with a Malayan pangolin (*Manis javanica*) coronavirus [2]. The latter, like the masked palm civet (*Paguma larvata*) in the 2002-2003 epidemic, is believed to have acted as an intermediate host between bats and humans to give rise to SARS-CoV-2, which is highly contagious in humans (See Focus: Bats and coronavirus emergence).

This is not the first time that bats have been in the spotlight. We have to go back to 1911 for the first mention of a virus isolated from bats. At the time, rabies was the subject of interest and it was discovered that it was transmitted by the common vampire bats of Brazil. After a long period of oblivion, it was rediscovered during the years 1990-2000 in the framework of health surveillance programmes that **bats** are the **natural hosts** of many **emerging viruses** such as henipaviruses (Hendra and Nipah), filoviruses (Ebola) and coronaviruses (SARS) [3] (Figure 1). Unexpectedly, they are found to be unaffected by most of these pathogens. It has even been demonstrated, particularly for the Hendra and Nipah viruses, that they can **withstand viral loads** that are normally lethal in other mammals [4].

## 2. Bats and viruses?

### 2.1. Bats account for a quarter of all mammalian species

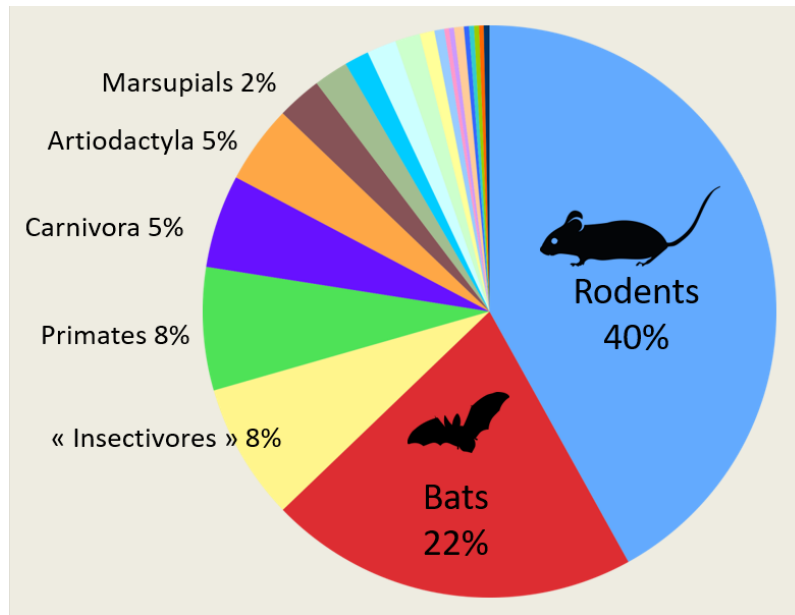


Figure 2. The order Chiroptera (bats) accounts for nearly a quarter of mammalian species. [Source: Aranae, Public domain, via Wikimedia Commons]

Bats are the only flying mammals grouped in the order Chiroptera, whose name comes from the Greek *kheir*, "hand" and *pteron*, "wing" meaning "that flies with its hands". This order includes a large number of species currently estimated at more than 1 428 or about a quarter of the 6 495 known mammalian species, placing it **second only to the order of Rodents** (Figure 2).

A recent revision of the order of Chiroptera based on molecular data has recast it into **two new suborders** that are more phylogenetically coherent (See: Focus [Bats and Coronavirus Emergence](#)) :



Figure 3. Spectacled flying foxes (*Pteropus conspicillatus*) in Cairns, Australia. They live mainly in the canopy of tropical rainforests. [Source: © François Moutou]

**Yinpterochiroptera** (Pteropodiformes), which includes tropical fruit bats or flying foxes (Figure 3);

The **Yangochiroptera** (Vespertilioniformes) which includes all microchiroptera except five families.

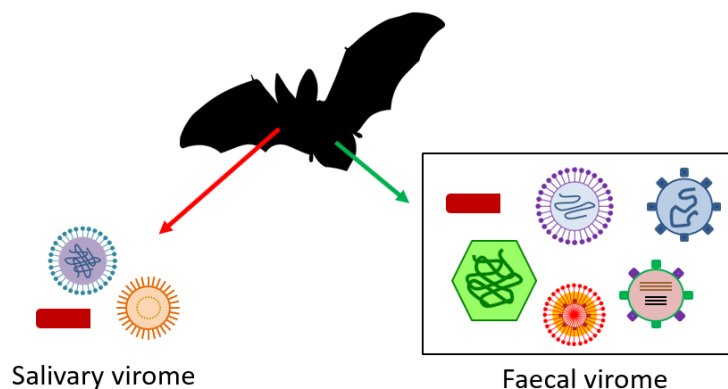
## 2.2. A very wide variety of ecological niches



*Figure 4. Lesser horseshoe bat (Rhinolophus hipposideros) in flight. It prefers hedgerows made up of grazed meadows interspersed with wooded hedges. [Source: © Louis-Marie Préau]*

Bats display an **exceptional diversity of species** that are widespread on all continents except the North and South Poles and occupy a very wide **variety of ecological niches** (Figures 3 & 4). As regards their **diet**, they are mainly frugivorous or insectivorous, but they may also be nectarivorous, pollinivorous, carnivorous (fish, amphibians, small mammals), omnivorous and haematophagous. This last diet concerns only three species of bats called vampires, located in tropical areas of the American continent. Although they rarely attack humans, these vampires are the object of unjustified fears among the public. Nevertheless, they can transmit the rabies virus by ingesting the blood of mammals. Thus, before going any further in the presentation, we can see that bats are a very favourable "breeding ground" for the **multiplication, exchange and spread of viruses**.

## 2.3 What are bat viromes?



*Figure 5. Analysis of different bat viromes. [Source: Author's figure]*

The relatively recent rediscovery of bat/virus links will spark interest among researchers in this new way of approaching diseases from an **ecological and health** perspective. In addition to this interest, recent advances in investigative methods will be added to this craze, using **metagenomic** and high-throughput sequencing **approaches** that make it possible to analyse all the viral genomes (virome) contained in a biological sample in record time and without the need for culture steps. All of this will lead to an acceleration of study programmes whose objectives are to improve knowledge of bat **viromes** (Figure 5). Campaigns will thus be launched to collect samples as diverse as guano (faeces), urine, oral or anal swabs, and even organs in countries where bat sacrifice is authorized [\[5\]](#).

Thanks to these samples, a large number of **viral sequences** were identified, some of which were found to be similar to those of many viruses known to be pathogenic to humans [\[6\]](#). Nevertheless, beware not to conclude, as has sometimes been done rather hastily, that bats are responsible for all the viral diseases that affect humans! Although these methods have brought significant advances in our knowledge of the links between viruses and bats, we must nevertheless remain cautious in interpreting the



considerable mass of data obtained, given the **weakness of the means of analysis**.

However, it is surprising to note that all these advances have confirmed simple observations made in 1974, which already revealed the propensity of bats to host a wide variety of RNA and DNA viruses [7].

## 2.4. Are bats "virus strain"?

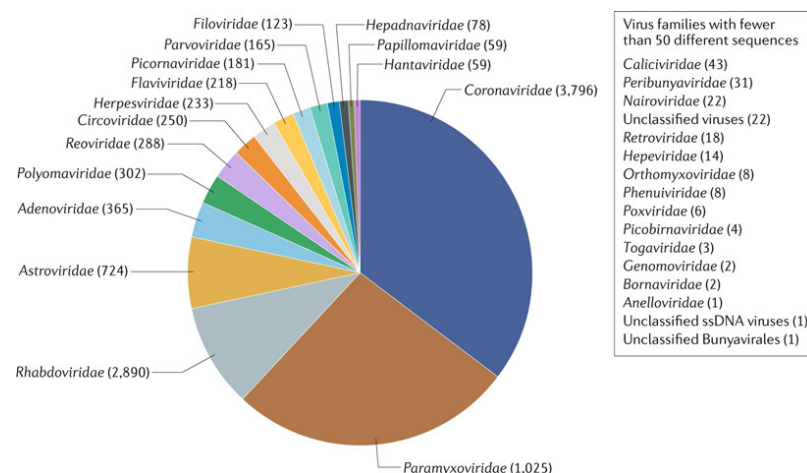


Figure 6. Diversity of viruses found in bats. Coronaviruses are the most numerous, but studies are only just beginning. [Source: Diagram by Letko et al. [11] Copyright / link: doi: 10.1038/s41579-020-0394-z]

Although Rodents are the 1<sup>st</sup> order in number of species among Mammals, a comparative study [8] of the number of **zoonotic viruses** present in Rodents and Chiroptera has shown that their numbers are higher in Rodents, 68 versus 61, but that the ratio of the total number of viruses per species puts Chiroptera at the top (1.79 versus 1.48). More recently, a study by Peter Daszak and colleagues published in the journal *Nature* [9] showed that the total number of viruses infecting a mammalian species can be used to predict the proportion of viruses capable of causing zoonoses. One of the conclusions of this work is that bats proportionally harbour a **higher number of zoonotic viruses** than in all other orders of mammals.

With regard to coronaviruses in particular, another large comparative study [10] was conducted in more than 19,000 animals belonging to bats, rodents and non-human primates. It showed that **98% of the coronaviruses** found came from bats. A massive and diverse presence since, out of one hundred types of coronavirus identified, 91 came from Chiroptera. The proportion of individuals positive to a coronavirus was 8.6% in bats and 0.2% in other animals. Extrapolating these results to all species of bats, they would be carriers of no less than **3,200 coronaviruses** throughout the world. This number was recently re-evaluated at 3,796 (Figure 6) [11]. Bats therefore seem to have special abilities.

Nevertheless, all this should be put into perspective because **sampling bias** exist in these studies. The order of Chiroptera, with its 1,428 species, occupies the second place among Mammals, and bats are inevitably at the forefront of the scene. Recently, researchers have shown that by going beyond mammals and including birds, the risk of viral zoonoses remains **homogeneous** regardless of whether the host species belong to the avian or mammalian orders, and thus the number of zoonoses per taxonomic order increases with species abundance [12]. Thus, for bats and rodents, the high number of zoonotic viruses is simply related to the **specific richness of the two orders** they represent.

In fact, explanations of the **special** role that bats play in viral emergences are more likely to be sought in terms of their **particular ecoethology**, their unusual physiological and immune characteristics, and also their ability to exchange RNA viruses more intensely than in other animal species. Finally, we must add the way in which **humans**, through their action on ecosystems, **create favourable conditions** for bringing all these elements into synergy.

## 3. Why are bats preferred hosts for pathogenic viruses?

### 3.1. Viruses and bats have been living together for a long time

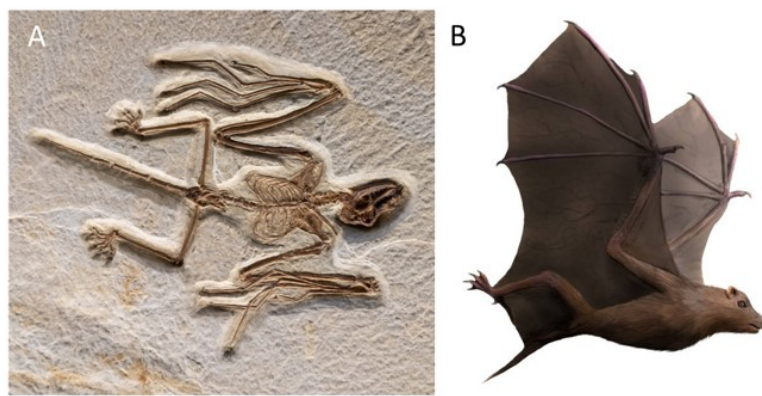


Figure 7. Age of bats. A, fossil of *Onychonycteris finneyi*, one of the oldest chiropteran fossils (Royal Ontario Museum) dating back 52.5 million years (Eocene). It was discovered in Wyoming, North America. This bat flew but was also able to climb trees. It hunted insects by using its sight and sense of smell as it was not yet equipped with the echolocation system. [Source: A, Matthew Dillon, CC BY 2.0, via Flickr]. B, probable representation of *O. finneyi*. [© N. Tamura; licence CC BY-SA]

The **virus/bat cohabitation** may have been established a very long time ago, since the oldest known fossil bats appeared with certainty in the Eocene more than 50 million years ago (Figure 7). Despite the Cretaceous-Tertiary biological crisis that occurred only 10 million years earlier, the diversity of bats in the **Eocene** is already remarkable. A recent publication [\[13\]](#) has confirmed the antiquity of the Chiroptera and shed new light on the origin of bats, which had until then been an enigma. By comparing the genomes of six bat species with those of other mammalian species, the researchers have shown that Chiroptera are indeed part of the **laurasiatheran** family, a super-order of placental mammals but that they share a common ancestor with the clade of *Fereuungulata* which groups together 5 orders (camels, pigs, cetaceans, horses, rhinoceroses, carnivores and pangolins) from which they have separated, pushing back the date of appearance of the Chiroptera to **more than 65 million years**.

### 3.2. A long period of co-evolution between viruses and bats

Viruses have thus had a very long time to adapt to their Chiropteran hosts and **co-evolve** intimately. A slow selection of the viruses' capacities to infect their host took place, leading to increasingly close **viral adaptation** to certain molecules present on the surface of bat cells. Since these molecules act as receptors, they will play a crucial role in the penetration of the virus into the host cells. Moreover, being involved in a number of fundamental physiological processes, these **receptor molecules** have remained highly conserved in the animal world. This explains the ease with which the viruses play on species barriers and circulate rapidly among mammalian hosts.

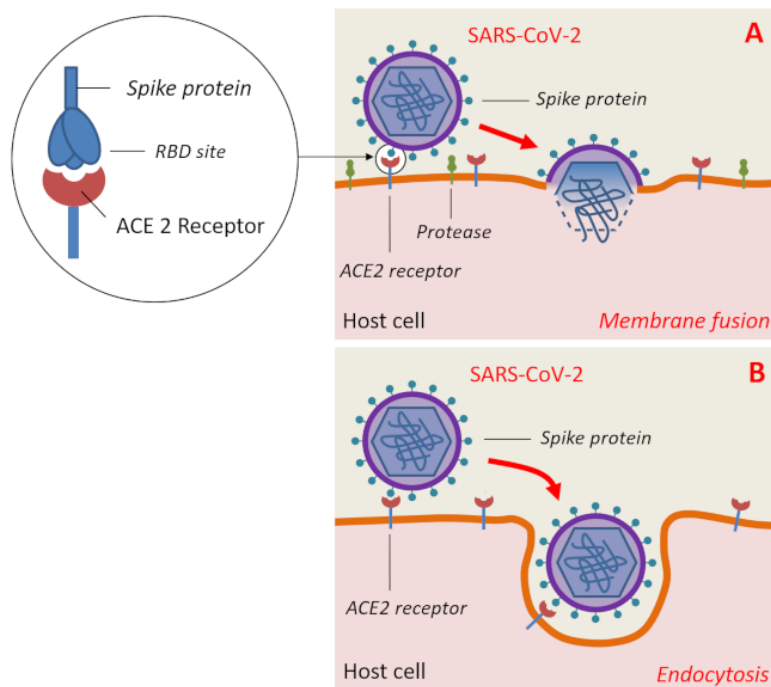


Figure 8. After Spike protein binding of SARS-CoV-2 to the host cell receptor consisting of the angiotensin I converting enzyme 2 (ACE2) and activation by cleavage of Spike by a membrane protease, fusion of the viral complex takes place directly on the cell surface (A). In the absence of protease, the virus enters the cell by endocytosis (B). [Source: Author's figure]

In the case of SARS-CoV-2, the receptor was rapidly identified as **angiotensin I converting enzyme 2 (ACE2)** (Figure 8). Involved in the regulation of blood pressure, is widely distributed in vertebrates, and is found on the cell surface of many tissues and organs (lungs, heart, arteries, kidney and digestive system). In infection, it acts as a lock and interacts with the key represented by the viral protein S (for *Spike* which means spicule). It is the spicules that give the virus its crowning glory, hence its name coronavirus.

However, the key (**S protein**) must still have mutagenically acquired a specific amino acid sequence in its *receptor binding* domain (RBD) to the human ACE2 receptor as well as a specific site of cleavage by host enzymes so that SARS-CoV-2 may infect human cells [14].

These **mutations** were presumably acquired by the bat coronavirus during passage through **intermediate hosts** to result in SARS-CoV-2. In addition to humans, the latter is capable of infecting other mammals such as primates (Macaque monkeys), certain species of deer and cetaceans, domestic cats, tigers, golden hamsters, ferrets, mink and domestic dogs. Apart from Mammals, other classes of vertebrates do not seem to be affected [15].

### 3.3. Flying, essential to the links between bats and viruses



Figure 9. Greater horseshoe bat (*Rhinolophus ferrumequinum*) in flight. [Source: © Louis-Marie Préau]

Among the adaptations that have made the success of the Chiroptera, **the acquisition of flight** during evolution is undoubtedly the most remarkable (Figure 9). It appears that flight played an essential role in the links between bats and viruses. In addition to the fact that it is an excellent means of movement for bats, it will contribute to the **spread of viruses** over large areas and in very varied ecosystems. For example, the geographical distribution of viruses of the genus *Henipavirus* has been found to overlap closely with that of bats of the genus *Pteropus*, with animal and human henipaviruses having been reported in Australia, Bangladesh, India, Malaysia and Singapore.

More unexpectedly, it was realized that flight, by greatly increasing the metabolism (15 to 16 times compared with the 2 times of most birds) and the bat's body temperature ( $>38^{\circ}\text{C}$ ), induced a response similar to that of a **feverish state**. However, fever is a natural defence mechanism used by endothermic animals to inhibit the growth of pathogens and stimulate their immunity. Thus, by inducing a more or less permanent feverish state, flight would contribute to making bats more **resistant to viral attacks** [16].

### 3.4. Breathing and oxidative stress

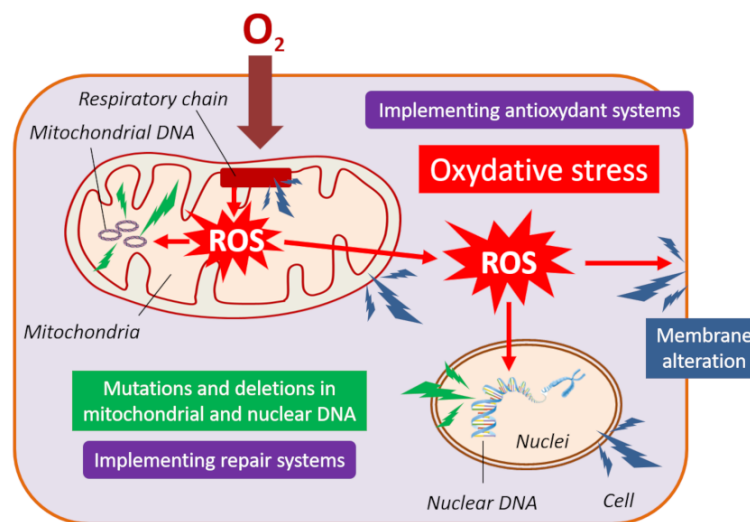


Figure 10. The production of reactive oxygen species (ROS) in the mitochondrial respiratory chain induces oxidative stress responsible for cell level alterations in membrane lipids, proteins and DNA. To protect itself, the cell has antioxidant and repair systems. [Source: Author's figure]

During flight, bats consume four times more oxygen, which generates a large quantity of reactive oxygen species (ROS) at the level of the mitochondrial respiratory chain, causing intense **oxidative stress** (Figure 10). The latter usually causes significant damage to cellular constituents, including DNA, but bats seem to escape it. In fact, bats have selected particularly effective **mitochondria** and **antioxidant systems** to support the high energy demand required by flight and protect themselves from the effects of oxidative stress [17]. When the damage is done, bats can rely on a high-performance **DNA repair system** [18]. Since



many pathogens generate oxidative stress in the initial stages of infection and mitochondria have an increasingly recognized role in the immune system, these adaptations, which were slowly selected by Chiroptera over the course of evolution, have had beneficial effects on their **immunity** and **pathogen control** [19].

### 3.5. Exceptional longevity conducive to virus persistence

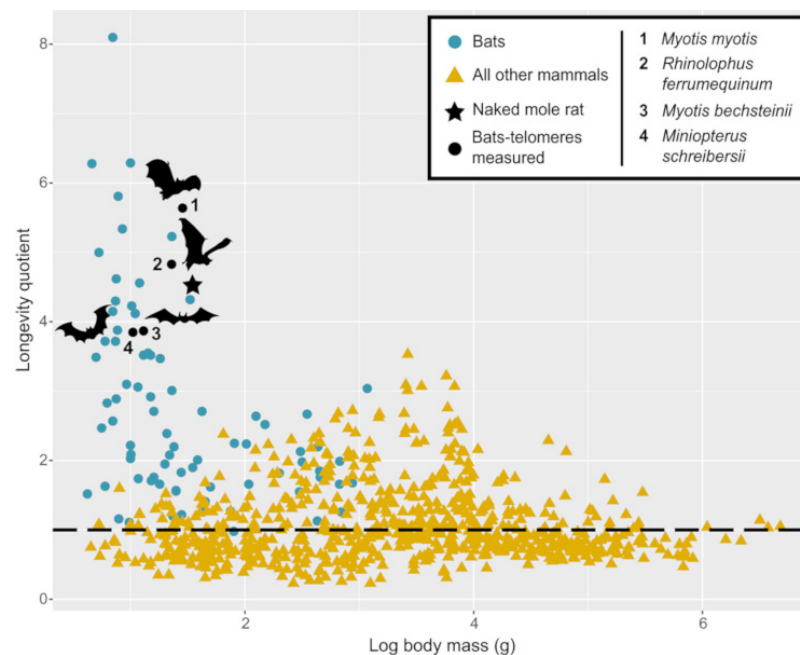


Figure 11. Longevity quotient (ratio of observed to estimated longevity) for 779 mammalian species as a function of body weight (in grams). The black dashed line indicates a quotient = 1. Most bats have a high longevity as a function of their body mass (blue dots), as in the case of one rodent species, the naked mole rat (black star). The relationship between telomere length and age was estimated for bat species represented by silhouettes. [Source Foley et al. [20], CC BY-NC 4.0 / Link: <https://advances.sciencemag.org/content/4/2/eaao0926>]

At the same time, the viruses would have gradually become accustomed to their chiropteran host and would have had to lower their virulence level. In other words, everyone learned to live together harmoniously. Thus, it can be seen that many life traits in bats are conducive to the **persistence of viruses**.

We saw earlier that the bat manages to moderate oxidative stress, which generally leads to chronic inflammation and accelerated aging. Similarly, the progressive shortening of telomeres (chromosome ends), which normally causes senescence and the appearance of cancer, has not been observed in bats [20]. Bats thus show **exceptional longevity** (Figure 11) with few signs of senescence and a negligible rate of cancer. Out of 19 mammalian species that live proportionally longer than humans, taking their body size into account, 18 are bats, with a record held by a Brandt's bat (*Myotis brandtii*), which, at a weight of 7 g, has exceeded the age of 41 years. This longevity is conducive to the persistence of viruses in individuals and to long-term viral exchanges between generations of juveniles and adults.

### 3.6. Lethargy and torpor



Figure 12. Greater horseshoe bat in hibernation. A, colony of Greater horseshoe bats; B, Greater horseshoe bat (*Rhinolophus ferrumequinum*) in lethargy enveloped in its wings (we can see the nasal leaf which allows the concentration of ultrasounds emitted by the nostrils for echolocation deployed in active phase). [Source: © Marc Pihet]

Another factor favourable to the persistence of viruses concerns the states of **lethargy** or **torpor** into which Chiroptera can enter (Figures 12 & 13).

Lethargy is a strategy used by bats in temperate countries to survive the insect shortage that occurs during cold seasons while other animals such as birds choose to migrate to warmer climates.



Figure 13. Lethargic Lesser horseshoe bat (*Rhinolophus hipposideros*) passively hanging from the wall by its claws. [Source: © Marc Pihet]

Thus during **hibernation**, which lasts several months, the bat falls into a state of profound lethargy that is accompanied by hypothermia and an extreme slowing of its metabolism in order to save energy. A weakening of the immune defences is associated; it is quite favourable to the maintenance of viruses. This explains the **inter-seasonal transmission of viruses**. As for tropical bats that do not hibernate, it has been observed that they periodically fall into states of daytime torpor, which are accompanied by a reduction in their metabolism as during hibernation [\[17\]](#).

### 3.7. Importance of living together

Viral persistence can also be expressed on an individual level, as well as on a collective level. Chiropterans have a strong propensity to group together in **colonies** of hundreds or even thousands of individuals of different ages and sometimes of different species. The largest known concentration of mammals is found in the *Bracken Cave* in Texas, which concentrates more than 20 millions of Brazilian free-tailed bats (*Tadarida brasiliensis mexicana*) (Figure 14). It takes at least 3 hours for the entire colony to emerge from the cave!



Figure 14. A, Bracken Cave (Texas, USA) which hosts one of the largest bat colonies in the world with an estimated 20 millions of Brazilian free-tailed bats gathered from March to October. B, Brazilian free-tailed bat (*Tadarida brasiliensis*) [Source: A, photo Jonathan-Alonzo, photo courtesy of Bat Conservation International / B, Michael Durham Minden, photo courtesy of Bat Conservation International].

During these aggregation phenomena, it is obvious that viruses are transmitted very easily between bats, either by mutual licking of their hairs, which are frequently soiled by urine or faeces, or by **aerosolisation** of biological liquids (urine, saliva), which are good carriers for viral diffusion. To move around or hunt at night, some bats use **echolocation** (See Focus: [Echolocation](#)) which mobilizes the ear, nose and throat and generates aerosols from secretions of the nasal mucosa and saliva, the preferred sites for viruses. This faculty acquired during evolution consists of emitting ultrasounds to create sound "images" in an environment without light.

In these groupings, it has been well shown that the nature and size of colonies play an important role in viral maintenance and the appearance of new variants. It is thought that **viral exchanges** between adults and juveniles promote **chronicity of infection**, whereas between individuals of different species, **viral diversity** increases. Researchers are now wondering whether this habit of living in sympatry may be the determining factor that has led bats to tolerate viruses while developing **unique immune capacities**, aspects of which have only recently begun to be identified.

### 3.8. Unique immune abilities

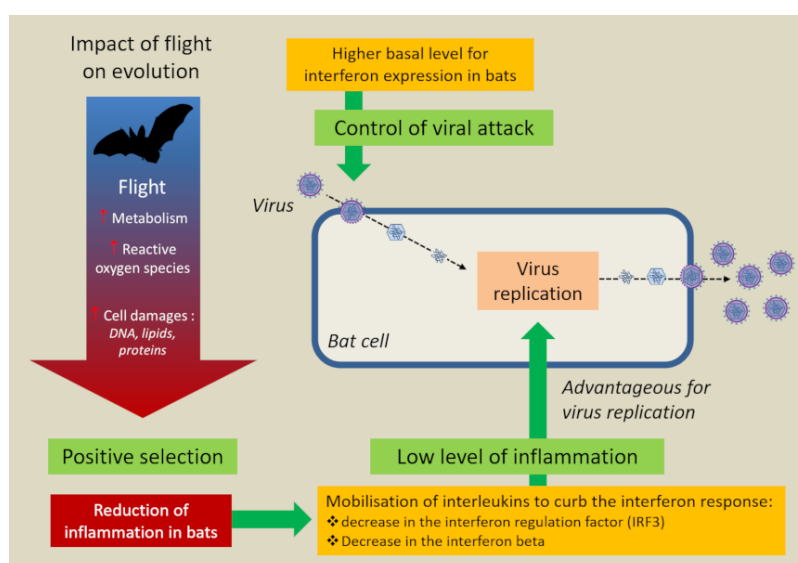


Figure 15. Flying induces in bats unique immune capacities designed to control the viral attack and the resulting inflammatory reaction. [Source: Author's Figure]



Normally, humans and most other mammals respond to a viral attack by activating their immune system at the time of infection. This is not the case in bats, which maintain this system **permanently but at low noise** levels so that it can quickly become more powerful in the event of infection (Figure 15). In fact, an initial inflammatory response makes it possible to send **cytokines** (interferons) that target the pathogenic agent as soon as it arrives, followed by a second response in which **interleukins** are used to **temper the inflammation** in order to prevent its deleterious effects on the host. In fact, it is flight, an intense and very pro-inflammatory activity, that is thought to have induced this unique ability to prevent the onset of exacerbated inflammation [18]. The latter corresponds to the famous cytokine storm evoked during the COVID-19 pandemic, which provokes a disproportionate inflammatory reaction in some patients and which resuscitators try to control, like bats, because it threatens the patient's vital prognosis [21].

In fact, bats seem capable of **restricting** their **immune response** to pathogens with which they share a long evolutionary history in order to limit the immunopathological consequences of an infection [22]. A kind of non-aggression pact seems to have been established between them and viruses.

Recent analysis of six bat genomes [13] has shown a wide variety of **endogenous viruses**, which tends to confirm this state of tolerance towards viruses recognised as elements of the bat self. It also revealed the concentration of the inflammatory response on a limited number of genes and the existence of new genes involved in **tolerance** to **viral infections**. This study aims to better understand how bats tolerate coronavirus infections.

## 4. Are bats responsible for viral outbreaks?

The recognition of the role of bats in viral epidemics presents the risk of bats being responsible for them and thus of considering their **eradication as a solution to the risk of infection**. This reaction, which is unfortunately intuitive, would prove to be totally inappropriate and even **prejudicial** to human health. It has already been tested in Uganda where, as part of campaigns to prevent Marburg virus infections, destruction of fruit bats has been carried out in some mines. This has resulted in re-invasion of these sites by susceptible bats and multiple reintroductions of the virus into new connected populations.

Reacting like this means forgetting that Chiropterans are **key species** in the functioning of ecosystems. In tropical environments, they play a significant role in the pollination of plants and the long-distance dissemination of seeds. Humans benefit by consuming them and using their guano as fertilizer. As for insectivorous bats, they play a major role in regulating insect populations and thus contribute to a reduction in the use of pesticides. Very sensitive to changes in their environment, bats are excellent **indicators of the health of our environment**.

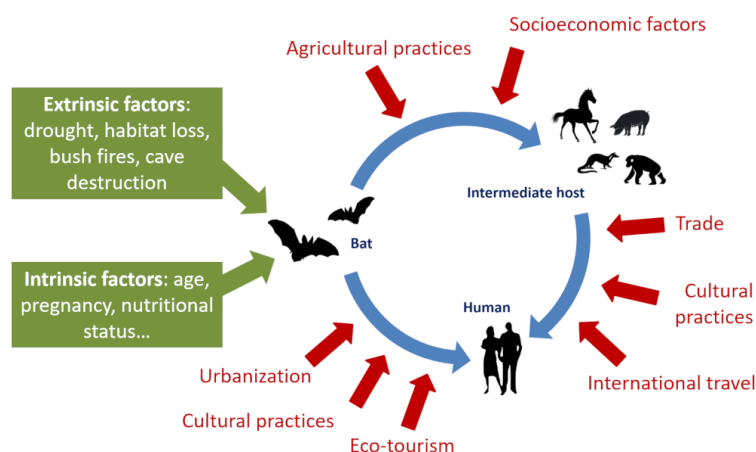


Figure 16. Factors favouring zoonoses. [Source: Author's figure]

The causes of epidemics are rather to be found in the **disruption** of natural **ecosystems** inflicted by **human activities**: intensification of agricultural practices leading to deforestation and habitat fragmentation, habitat degradation and rapid urbanization [23] (Figure 16). These activities encroach on areas that have long remained wild and bring bat populations closer to human habitats and domestic animal farms [24]. In addition, there is the unnatural grouping under deplorable **conditions** of live wild or domestic animals intended for sale on the markets, which are veritable cauldrons of emerging viruses. To avoid this, an easy and quick measure would be to apply **strict controls** on these live animal markets. In the longer term, human beings should be encouraged to make **profound changes in their eating habits**.

In a more comprehensive way, it will be necessary to act on the **risk factors** that expose humans to wildlife and bats. The COVID-19 pandemic is there to remind us of this. It made it clear that controlling these risks requires **close collaboration**

between the fields of human health, animal health and ecosystem health. In other words: doctors, pharmacists, veterinarians and ecologists, as well as economists and lawyers, must work together to promote an **ecology of health**, an essential approach to prevent future epidemics and prevent them from turning into health crises (See [Viral pandemics of the modern era](#)).

## 5. Messages to remember

Bats are **natural hosts** for many emerging viruses, but are unaffected by most of them.

Bats are the **preferred hosts of viruses** because of their **diversity** of species, 2<sup>nd</sup> order in Mammals, diets, and ecological niches.

Research is being conducted on the **virome** (set of viral genomes) of bats, which shows that they are **not directly responsible** for human viral diseases.

Their appearance dates back more than 65 million years, which has given them time to **co-evolve closely** with viruses.

The success of Chiropterans is due to their unique **adaptations**: flight and echolocation abilities, exceptional longevity, ability to enter states of lethargy or torpor, gregarious instinct and unique immune system that have contributed to their **wide tolerance to infections**

Chiropterans are key species in the functioning of ecosystems and excellent **indicators of the health** of our environment.

The causes of epidemics are rather to be found in the disruption of natural ecosystems due to **uncontrolled human activities**.

To prevent new epidemics, it is imperative to act on the **risk factors** that expose humans and wildlife.

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## Notes and References

**Cover image.** Greater mouse-eared bat (*Myotis myotis*) in flight. [Source: © Louis-Marie Préau, [www.louismariepreau.com](http://www.louismariepreau.com)]

[1] Zhou P, Yang XL, Wang XG, Hu B, Zhang L, Zhang W, Si HR, Zhu Y, Li B, Huang CL, Chen HD, Chen J, Luo Y, Guo H, Jiang RD, Liu MQ, Chen Y, Shen XR, Wang X, Zheng XS, Zhao K, Chen QJ, Deng F, Liu LL, Yan B, Zhan FX, Wang YY, Xiao GF & Shi ZL. (2020). A pneumonia outbreak associated with a new coronavirus of probable bat origin. *Nature*, **579** (7798), 270-273. <doi: 10.1038/s41586-020-2012-7>.

[2] Xiao K, Zhai J, Feng Y, Zhou N, Zhang X, Zou J-J, Li N, Guo Y, Li X, Shen X, Zhang Z, Shu F, Huang W, Li Y, Zhang Z, Chen R-A, Wu Y-J, Peng S-M, Huang M, Xie W-J, Cai Q-H, Hou F-H, Chen W, Xiao L & Shen Y. (2020). Isolation of SARS-CoV-2-related coronavirus from Malayan pangolins. *Nature*, **583** (7815), 286-289. <doi: 10.1038/s41586-020-2313-x>.

[3] Calisher CH, Childs JE, Field HE, Holmes KV & Schountz T. (2006). Bats: important reservoir hosts of emerging viruses. *Clin. Microbiol. Rev.*, **19** (3), 531-545. <doi:10.1128/CMR.00017-06>.

[4] Middleton DJ, Morrissy CJ, van der Heide BM, Russell GM, Braun MA, Westbury HA, Halpin K & Daniels PW. (2007). Experimental Nipah virus infection in pteropid bats (*Pteropus poliocephalus*). *J. Comp. Pathol.*, **136** (4), 266-272. <doi: 10.1016/j.jcpa.2007.03.002>.

[5] Hu D, Zhu C, Wang Y, Ai L, Yang L, Ye F, Ding C, Chen J, He B, Zhu J, Qian H, Xu W, Feng Y, Tan W & Wang C. (2017). Virome analysis for identification of novel mammalian viruses in bats from Southeast China. *Sci. Rep.* **7** (1), 10917. <doi: 10.1038/s41598-017-11384-w>.

[6] Drexler JF, Corman VM, Müller MA, Maganga GD, Vallo P, Binger T, Gloza-Rausch F, Rasche A, Yordanov S, Seebens A,



Oppong S, Adu Sarkodie Y, Pongombo C, Lukashev AN, Schmidt-Chanasit J, Stöcker A, Carneiro AJ, Erbar S, Maisner A, Fronhoffs F, Buettner R, Kalko EK, Kruppa T, Franke CR, Kallies R, Yandoko ER, Herrler G, Reusken C, Hassanin A, Krüger DH, Matthee S, Ulrich RG, Leroy EM & Drosten C. (2012). Bats host major mammalian paramyxoviruses. *Nat. Commun.*, **3**, 796. <Law: 10.1038/ncomms1796>.

[7] Sulkin SE & Allen R. (1974). *Virology*. Vol. 8, Basel: Melnick JL, Karger.

[8] Luis AD, Hayman DT, O'Shea TJ, Cryan PM, Gilbert AT, Pulliam JR, Mills JN, Timonin ME, Willis CK, Cunningham AA, Fooks AR, Rupprecht CE, Wood JL & Webb CT. (2013). A comparison of bats and rodents as reservoirs of zoonotic viruses: are bats special? *Proc. Biol. Sci.* **280** (1756), 20122753. <Law: 10.1098/rspb.2012.2753>.

[9] Olival KJ, Hosseini PR, Zambrana-Torrel C, Ross N, Bogich TL & Daszak P. (2017). Host and viral traits predict zoonotic spillover from mammals. *Nature*, **546** (7660), 646-650. <doi: 10.1038/nature22975>.

[10] Anthony SJ, Johnson CK, Greig DJ, Kramer S, Che X, Wells H, Hicks AL, Joly DO, Wolfe ND, Daszak P, Karesh W, Lipkin WI, Morse SS; PREDICT Consortium, Mazet JAK & Goldstein T. (2017), Global patterns in coronavirus diversity. *Virus Evol.* **3** (1), vex012. <Law: 10.1093/ve/vex012>.

[11] Letko M, Seifert SN, Olival KJ, Plowright RK & Munster VJ. (2020). Bat-borne virus diversity, spillover and emergence. *Nat. Rev. Microbiol.* **18** (8), 461-471. <doi: 10.1038/s41579-020-0394-z>.

[12] Mollentze N & Streicker DG. (2020). Viral Zoonotic Risk Is Homogenous Among Taxonomic Orders of Mammalian and Avian Reservoir Hosts. *Proc. Natl. Acad. Sci. USA*, **117** (17), 9423-9430. <doi: 10.1073/pnas.1919176117>.

[13] Jebb D, Huang Z, Pippel M, Hughes GM, Lavrichenko K, Devanna P, Winkler S, Jermin LS, Skirmuntt EC, Katzourakis A, Burkitt-Gray L, Ray DA, Sullivan KAM, Roscito JG, Kirilenko BG, Dávalos LM, Corthals AP, Power ML, Jones G, Ransome RD, Dechmann DKN, Locatelli AG, Puechmaile SJ, Fedrigo O, Jarvis ED, Hiller M, Vernes SC, Myers EW & Teeling EC. (2020). Six reference-quality genomes reveal evolution of bat adaptations. *Nature*, **583**, 579-584. <doi: 10.1038/s41586-020-2486-3>.

[14] Zhang T, Wu Q & Zhang Z. (2020). Probable Pangolin Origin of SARS-CoV 2 Associated with the COVID-19 Outbreak. *Curr. Biol.* **30** (7), 1346-1351.e2. <doi: 10.1016/j.cub.2020.03.022>.

[15] Damas J, Hughes GM, Keough KC, Painter CA, Persky NS, Corbo M, Hiller M, Koepfli KP, Pfenning AR, Zhao H, Genereux DP, Swofford R, Pollard KS, Ryder OA, Nweeia MT, Lindblad-Toh K, Teeling EC, Karlsson EK & Lewin HA. (2020). Broad host range of SARS-CoV-2 predicted by comparative and structural analysis of ACE2 in vertebrates. *Proc. Natl. Acad. Sci. U.S.A.* 2020 Aug 21:202010146. <doi: 10.1073/pnas.2010146117>.

[16] O'Shea TJ, Cryan PM, Cunningham AA, Fooks AR, Hayman DTS, Luis AD, Peel AJ, Plowright RK & Wood JLN. (2014). Bat flight and zoonotic viruses. *Emerg. Infect. Dis.* **20** (5): 741-745. <doi:10.3201/eid2005.130539>.

[17] Brook CE & Dobson AP. (2015). Bats as special reservoirs for emerging zoonotic pathogens. *Trends Microbiol.* **23** (3), 172-180. <doi: 10.1016/j.tim.2014.12.004>.

[18] Zhang G, Cowled C, Shi Z, Huang Z, Bishop-Lilly KA, Fang X, Wynne JW, Xiong Z, Baker ML, Zhao W, Tachedjian M, Zhu Y, Zhou P, Jiang X, Ng J, Yang L, Wu L, Xiao J, Feng Y, Chen Y, Sun X, Zhang Y, Marsh GA, Cramer G, Broder CC, Frey KG, Wang L-F & Wang J. (2013). Comparative analysis of bat genomes provides insight into the evolution of flight and immunity. *Science*, **339** (6118), 456-460. <doi: 10.1126/science.1230835>.

[19] Banerjee A, Baker ML, Kulcsar K & Misra V, Plowright R, Mossman K. (2020). Novel insights into immune systems of bats. *Front. Immunol.* **11**, 26. <doi: 10.3389/fimmu.2020.00026>.

[20] Foley NM, Hughes GM, Huang Z, Clarke M, Jebb D, Whelan CV, Petit EJ, Touzalin F, Farcy O, Jones G, Ransome RD, Kacprzyk J, O'Connell MJ, Kerth G, Rebelo H, Rodrigues L, Puechmaile SJ & Teeling EC. (2018). Growing old, yet staying young: The role of telomeres in bats' exceptional longevity. *Sci. Adv.* **4** (2), eaao0926. <10.1126/sciadv.aao0926>.

[21] Kacprzyk J, Hughes GM, Palsson-McDermott EM, Quinn SR, Puechmaile SJ, O'Neill LAJ & Teeling EC. (2017). A potent anti-inflammatory response in bat macrophages may be linked to extended longevity and viral tolerance. *Acta Chiropter.* **19** (2), 219-228. <doi: 10.3161/15081109ACC2017.19.2.001>.

[22] Mandle JN, Schneider C, Schneider DS, Baker ML. (2018). Going to bat(s) for studies of disease tolerance. *Front Immunol.* **9** (2112). <doi: 10.3389/fimmu.2018.02112>.

[23] Gibb R, Redding DW, Chin KQ, Donnelly CA, Blackburn TM, Newbold T & Jones KE. (2020). Zoonotic host diversity

increases in human-dominated ecosystems. *Nature*, **584** (7821), 398-402. <doi: 10.1038/s41586-020-2562-8>.

[24] Afelt A, Frutos R & Devaux C. (2018). Bats, Coronaviruses, and Deforestation: Toward the Emergence of Novel Infectious Diseases? *Front. Microbiol.* **9**, 702. <doi: 10.3389/fmicb.2018.00702>.

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