



## ECOLOGICAL FACTORS OF TRANSMISSION, PERSISTENCE AND CIRCULATION OF PATHOGENS IN BAT POPULATIONS

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### ABSTRACT

The existence of bats is crucial for all ecosystem units as they fulfil numerous ecological roles. However, they are also considered to be natural reservoirs of a wide range of zoonotic microorganisms, especially viruses. In this review article we briefly summarize current knowledge about various ecological factors that facilitate bat pathogen dispersal and about the current approaches to monitoring viral communities present within bat populations. On the basis of the cited papers, we suggest that the increased focus on complex viral populations in bats and their interactions with other populations and the environment is necessary to fully comprehend the relationship between emerging infectious diseases, the environment and their toll on human health.

**Key words:** bats; ecology; reservoir; viruses; zoonoses

### INTRODUCTION

Bats belong to the mammalian order *Chiroptera*. Many species are ubiquitous; bats can be found on every continent except arctic regions and Antarctica [52]. Members of the order *Chiroptera* are the only known mammals capable of sustained flight. To this day, approximately 1,232 species of bats have been described [29, 49, 50].

The existence of bats is crucial for all ecosystem units, humans included. Bats fulfil numerous ecological roles [29]: they are important pollinators of fruit-bearing trees and play a role in the process of reforestation [29]. Insectivorous species are significant predators of insects, especially crop pests and nuisance insect species [29]. The guano of many bat species is collected due to its high nitrogen content and used as fertilizer [2].

However, bats are also considered to be natural reservoirs of a wide range of zoonotic microorganisms, especially viruses. These viruses include, but are not limited to, various species of the genus *Lyssavirus*, henipaviruses, coronaviruses (e. g. SARS-CoV) and filoviruses such as several species of the *Ebola* virus [7, 34, 39, 51, 54, 56];



Fig. 1. Hibernation of *Myotis dasycneme* together with *M. myotis*

there have been virus isolates from bats identified also as Rhabdoviruses, possibly a *Lyssavirus* labelled as Kotalahti bat *Lyssavirus* [38]. Novel viruses in bats are being identified quite often.

Bats are hosts also to a few pathogenic bacterial species, such as *Leptospira* spp. and *Bartonella* spp. [30]; various *E. coli* serotypes have also been isolated [1, 8, 11, 37]. In general, bats are not as prominent in carrying dangerous bacteria and transmitting them to humans, as they are in spreading dangerous viruses; however, these bacteria may constitute a potential threat to human health [2] whenever humans are exposed to bat carcasses or excretions.

In this review article we briefly summarize current knowledge about various ecological factors contributing to facilitate bat pathogen dispersal and the current approaches to monitoring viral communities present within bat populations.

### The order *Chiroptera* and its ecological influence

The order *Chiroptera* is unique among all other mam-

malian orders. Their anatomy, physiology and behaviour are specifically suited to their unparalleled way of life and their function within the ecosystem of the Earth is conditioned by these features. In this article we summarize the factors contributing to the bats' surprisingly high ability to spread dangerous viral pathogens, while causing massive spillover events.

### Colony size and gregarious social behaviour

Most bats live in groups with a high number of individuals at least for a certain period of time during one year (Figs. 1—2). Some authors describe a correlation between population size and persistence of pathogens in these populations [3, 41]; this has been observed in many cases. A study from 2012 [40], however, indicates that henipaviruses have been detected in an isolated bat population on an island near Africa, counting only a very few individuals. The number of individuals in this population does not reach a population threshold number necessary to keep the viruses circulating [40], nevertheless, it appears to persist in these bats.





Fig. 2. A group of *Barbastella barbastellus*



Fig. 3. A cluster of hibernating *Myotis myotis*





Fig. 4. *Pipistrellus pygmaeus*

### Patagium

Bats are capable of sustained flight due to the presence of this specialized anatomical structure; it is a thin skin membrane extending between the phalanges and pelvic limbs. Bats also wrap themselves in it to steady their internal environment during hibernation and rest (Fig. 3). The ability to fly is probably one of the most important factors when it comes to pathogen dispersal; during migration, bats cover long distances [12—14], excreting viruses along the way. What is more, Brook and Dobson [5] have proposed an indirect way, in which the ability to fly increases viral spillover from bats to other species. These authors' work highlights the fact that bats are evidently immune to intracellular infections, while succumbing, even population-wide in some areas, to extracellular pathogens. Brook and Dobson [5] attribute this phenomenon to a special metabolic adaptation involving the mitochondria which apparently enables both flight and an increased resistance to viral infections.

### Ways of obtaining nutrition

In order to be able to keep their aerodynamicity, bats need to ingest highly nutritious forms of sustenance, since

they cannot afford to consume large quantities of food at once [36] (Fig. 4). For this purpose, some insectivorous bats only swallow a part of the insects, while dropping the rest down to the ground, where these remains—along with the bats' saliva—are ingested by other animals [18, 36]. Frugivorous bats only chew at the fruit, swallowing the sugary juice and dropping the rest on the ground as well [36]. Bat species feeding on blood can transmit diseases to bitten individuals, such as rabies [35, 36].

### Anthropogenic and economic factors

The story of the frugivorous bats continues on the interface with humans. A fitting example of dangerous bat-human interface is date palm sap produce, date palm sap being a popular drink in Bangladesh [27]. Date palm sap is produced by tapping the date palm and collecting the sap in containers [27]. Frugivorous bats have learned to fly to these trees and lick the dripping sap, contaminating the raw product with urine [27, 33, 43]. Several preventive measures decreasing the risk of date palm sap have been proposed, on the other hand, their feasibility is questionable [27]. In many countries bats are sold at markets for

meat, which jeopardizes buyers, sellers, hunters and butchers alike [25]. Limiting the trade of bat meat is difficult, mainly due to economy in these regions [25, 55]. Bat guano collectors are also exposed to dangerous viruses present in the excretions [53].

### **Circannual cycle**

All of the European bat species undergo hibernation, which is influenced by the outer temperature [44]. There have been findings connecting hibernation to decreased immune function [4, 19], which facilitates the persistence of viral pathogens in infected individuals [4, 5, 19].

### **Longevity**

Bats can live for decades [12–14, 21]. The longer a reservoir organism lives and is active, the longer it is able to excrete pathogens; what is more, several authors [5, 47, 48] have connected their longevity with metabolic mechanisms facilitating the persistence of intracellular pathogens.

### **The importance of ecology in bat-borne pathogen research**

Wood et al. [57] in their work describe the interdependence of human health and the health of the ecosystem, and with an emphasis on bats as important reservoirs of emerging infectious diseases, these authors suggest a complex approach to studying zoonoses. Their idea is based on a case study involving bats as a source of RNA viruses transmitted to humans. The authors propose a comprehensive and holistic view of studying zoonoses based on systematic monitoring of the human-wildlife interface, i.e. the interactions between humans and wildlife, taking into account the dynamics of viral and reservoir species populations, but also other possible amplifiers of the diseases, such as livestock. They further emphasize the often neglected cultural and political background, which should support the research by spreading the news within the non-scientific public and issuing proper legislation. Preserving nature and reservoir species and protecting their environment while keeping to the proposed approach will, according to these authors, help minimize spillover of dangerous bat-borne viruses into humans.

### **Metagenomic analysis of viral populations in bats**

Modern findings in the field of molecular biology enable us to analyse samples in bulk in a relatively short time.

Metagenomic analysis facilitates the discovery of novel pathogens; it can be used to obtain genome sequences of complete viral populations from both environmental and biological samples [15, 28], such as mucosal swabs, blood clots etc. The main advantage of metagenomic analysis is the possibility to capture almost all (and often whole) viral sequences present in the analysed sample and thus to study viral populations (viromes) present in the infected organism. Such screening applied to bat guano samples, for instance, has the potential to reveal “old known” pathogens that have been the subject of chiropterologic studies in the past, along with completely novel (i. e. never before identified, or possibly new variations of known) viral taxa; these data may be useful for predicting the next potential grave spillover events [31]. There are several particular protocols for metagenomic analysis built on the same bioinformatic principle. With the advent of new generation sequencing (massively parallel sequencing methods), modifications were made to classic molecular-genetic methods in order to discover novel pathogens which had not been cultivated before [15, 22, 23, 26, 28, 32, 42, 46]. Sequence-Independent Single Primer Amplification [10] was developed by Reyes and Kim [45]; it allows for fast amplification of a viral genome present in the analysed sample in only a few steps [17]. This method has been modified several times since its first implementation [16, 20, 58] together with the development of new sequencing methods, which simplified the process. Froussard’s modification brought forth the so-called random-PCR, which combines reverse transcription and PCR using random hexamers labelled with known sequences used during the extension step; thus enough cDNA is produced for further cloning and sequencing [20, 58]. Depew et al. [16] modified this protocol so that viruses isolated on a single plaque are identifiable via HiSeq Illumina platform.

### **The influence of other species**

Parasitism is present in many mammalian species, and bats are no exception (Fig. 5). Even though parasites of bats do not transmit to humans in such a degree as viruses—maybe with the exception of some ticks, e. g. *Argas vespertilionis* [6]—bat parasites may have a direct impact on the ecology of bat and virus populations worldwide [24].

Some of the mentioned viral families have been detected also in small rodents [9], which may suggest another element of the viral ecological cycle.



Fig. 5. *Rhinolophus hipposideros* attacked by tick

## CONCLUSIONS

The papers cited in our review focus the attention of the professional public on the importance of interspecies relationships in Earth's ecosystems with regard not only to animal species, but also in connection with populations of infectious agents and their circulation within the environment. Several authors cited in this review report findings of various animal and insect viruses in the insectivorous

bats; the latter appear as a central meeting point connecting many arthropod, mammalian and other *Metazoan* species with the human race. It is plausible that by enabling dangerous viruses to persist in their populations, bats contribute to the spillover of these pathogens to species (including, but certainly not limited to, humans) for which they are highly virulent.

Based on the cited papers, we suggest that the increased focus on complex viral populations in bats and their in-



teractions with other populations and the environment is necessary to fully comprehend the relationship between emerging infectious diseases, the environment and their toll on human health. We assume that this necessity will increase as humans will continue to exploit parts of the world where these viruses have been circulating. Researchers studying viral populations should do so systematically, with a long-term focus on selected areas. There is currently no known method of exact prediction where or when another emerging infectious disease (EID) will appear [31]; however, with enough metagenomic data, it might be possible at least to presume and test which viral taxa are more or less likely to infect mammalian cells [31]. In order to achieve this goal, close cooperation of experts in ecology, zoology, microbiology, molecular biology, immunology and bioinformatics will be necessary; and last, but not least, also the cooperation of state legislation organs and public health officials.

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