



Review Surveying Bat-Hosted Adenoviruses and Herpesviruses: A Comprehensive Analysis

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Abstract: Bats have gained cumulative attention as potential reservoirs for viruses, being crucial to increase our ability to predict viral prevalence and transmissions, as well as support the possible management of future zoonotic episodes. Following the PRISMA standard systematic review protocols, we conducted a comprehensive search worldwide for scientific papers dealing with bathosted viruses of the Adenoviridae and Herpesviridae families. The search was completed using the Scopus, CABI, and SciELO, databases of bat-associated viruses of these two families as well as the Google Scholar search engine. Our search comprised a total of 2656 scientific papers. After a thorough review and screening of the papers, we selected for our study a total of 90 papers published between 1996 and 2022. We found marked taxonomic and spatial biases, the most studied bats being predominantly vespertilionids, rhinolophids, phyllostomids, and pteropodids, whereas other families (e.g., Natalidae, Noctilionidae, and Furipteridae) are still lacking information. The most studied areas are southern and east Asia, although there are large areas (north Africa, the Middle East, and all the way to central or northern Asia) still overlooked. Out of the total number of papers, as many as 55 identified bat-hosted Adenovirus (AdV) and 54 papers identified Herpesvirus (HSV). Our revision reveals the presence of AdVs in a total of 97 bat species from 42 genera and 11 families. The presence of HSVs is reported also in 109 bat species from 45 genera and 10 families. Although both AdVs and HSVs in general show a clear host specificity and parallel evolution with their hosts, these results also point to the potential of these viruses to cross, in some cases, species barriers.

Keywords: Adenoviridae; review; bibliographic analysis; Herpesviridae; Chiroptera

1. Introduction

Bats are increasingly recognized as natural reservoirs of a great diversity of viruses, some of them showing emerging zoonotic potential. Their host potential is attributed to intrinsic ecological characteristics shown by bats, such as long-distance dispersal capacity, longevity, complex social structures, and antiviral immune responses that effectively regulate virus spread while concurrently restricting potentially harmful inflammatory reactions, that



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Copyright: © 2024 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). somehow facilitate the spread and persistence of viruses within and among species [1–3]. Bats are a natural reservoir for many viruses, such as rhabdoviruses (e.g., Lyssavirus), henipaviruses (e.g., Hendra and Nipah viruses), coronaviruses (e.g., RATG13), or filoviruses (like Marburg virus), among others; some of these viruses have become relevant in recent years because of the severity of their effects when being transmitted to humans [2,4].

The viruses included in the family Adenoviridae (AdVs) are non-enveloped doublestranded DNA (dsDNA) viruses that can infect numerous vertebrate species. Their transmission occurs through a fecal–oral route and the inhalation of aerosols, affecting particularly the respiratory, ocular, and urinary tracts; the infection can be persistent in their hosts, with the production of low levels of virions lasting years [5,6]. AdVs are considered of clinical interest, since, although causing generally gastrointestinal infections in humans, they can provoke also severe infections in immune-compromised people.

AdVs are grouped into six genera according to the International Committee on Taxonomy of Viruses (ICTV): *Mastadenovirus* which primarily infects mammals, *Aviadnovirus* infecting birds, *Ichtadenovirus* infecting fish, *Testadenovirus* that targets turtles, and *Atadenovirus* and *Siadenovirus* that have a wide host spectrum [7]. The ICTV currently recognizes ten types of bat mastadenoviruses (https://ictv.global/taxonomy, accessed on 1 January 2023). However, several studies have detected a much higher number of putative AdVs that have not been formally classified by the ICTV [8].

The viruses included in the family Herpesviridae (HSVs) are enveloped and have dsDNA. They can infect invertebrate and vertebrate species with a transmission route through body fluids. The infection of HSVs is characterized by cell and tissue tropisms and by a persistent infection known as the latency phase. Under infection, the viral genome remains in the nucleus of the host cell throughout the whole life of the infected individual. The reactivation of the latent viruses can be triggered by stress, aging, or infections that decrease the immunocompetence of the host [9–11]. HSVs conform to a quite diverse group of viruses which are grouped into three subfamilies according to the ICTV: Alphaherpesviriniae, Betaherpesviriniae, and Gammaherpesviriniae, all using a wide spectrum of animal hosts.

The study of viruses has seen significant growth in recent decades, primarily driven by the increasing interest in their potential to trigger epidemics. This growth is likely also attributable to the substantial advancements in diagnostic abilities' developments in recent years, which have facilitated a faster identification of new emerging viruses [12]. Due to the putative relevance of bats as reservoirs of potentially concerning viruses, it is important to summarize the recent knowledge progress achieved on bat-related viruses (particularly, AdVs and HSVs). On the other hand, many questions still remain unsolved about the ecological and evolutionary relationships between bats and their host viruses. This review aims to address the current knowledge gaps and explore the direction of recent research efforts.

To this end, we conducted a comprehensive review of papers worldwide in which the occurrence of viruses of the families Adenoviridae and Herpesviridae were investigated in bats. These two particular viral families were selected due to their high diversity, their wide geographical distribution, and their capability of infecting a wide spectrum of vertebrates. The aims of this study are as follows: (1) summarize the bat species worldwide that are known to host AdVs or HSVs and (2) analyze the relations merging from our present knowledge of both viral families and their host bats worldwide.

The results of this study will contribute to identifying information gaps in our present understanding of the natural diversity of viruses present in wildlife.

2. Materials and Methods

2.1. Literature Review and Bibliometric Analyses

We followed the standard systematic review protocols PRISMA [13,14] to carry out a systematic search for scientific papers reporting the presence of AdVs and HSVs in bat species. The search was conducted using the Scopus, CABI, and SciELO databases, the database of bat-associated viruses (http://www.mgc.ac.cn/DBatVir/, accessed on 1 January 2023), and the search engine Google Scholar. Additionally, our search was complemented by additional publications present in the reference list of each paper that was initially included. The search utilized the keywords "Adenoviridae", "adenovirus", "Herpesviridae", "herpesvirus", "virome", and "bat". This comprehensive search was carried out up until the year 2022 (inclusively).

The original set was inspected and filtered, excluding all papers published in nonindexed journals, non-English language studies, experimental studies, and reviews. Papers using datasets in which bats were not identified at the species level were also excluded (Figure 1 and Table S1). The selected papers were thoroughly examined to determine their eligibility for the analysis and to extract 21 variables, which were categorized into (1) description of the papers; (2) fieldwork and bat characteristics; and (3) viral characteristics and detection methods (Table S2).



Figure 1. PRISMA 2020 flow diagram for the systematic review of adenovirus and herpesvirus (Adenovirus/Herpesvirus) in bats in the scientific literature.

The taxonomic and nomenclature of bats were based on Wilson and Mittermeier (2019) [15]. The conservation status of each species was obtained from the list of threatened species of the International Union for Conservation of Nature (IUCN) website (https://www. iucnredlist.org/, accessed on 1 May 2023). Viral taxonomy and nomenclature were based on the International Committee on Taxonomy of Viruses (ICTV). However, in most papers, the viruses were not identified and were categorized as "unassigned". In cases where information for other variables was missing, we attempted to contact to the corresponding author. When our attempts were unsuccessful, we replaced some missing information using online databases, like Genbank (https://www.ncbi.nlm.nih.gov/genbank/, accessed on 1 May 2023). Additionally, if multiple detection techniques were employed in the same individuals, we recorded the data and techniques that resulted in the highest number of detected viruses. In cases where no specific collection site was reported, we used the coordinates of the capital city of the state, province, or country mentioned in the paper. When dealing with studies that utilized sample pools, only pools containing individuals of a single species were considered. Finally, if the number of positive individuals for a particular virus was not specified, either by processing multiple samples or by not

providing information, it was assumed to be just "present", excluding these data only from the prevalence results, while the remaining variables without available data were marked

as "not completed". The relationship between the number of studied cases and the number of bats positive to either AdVs or HSVs was estimated for virus family and each country through a Spearman correlation, using the PAST 3.0 [16]. The main regions of study were determined based on the number of papers. We also conducted a spatial distribution network to analyze the geographical association between research teams and each case study, represented through a bipartite spatial network built with Geo Layout v.0.9.2.2 in the Gephi v. 0.9.3 software [17]. Temporal changes in the number of published papers were tested through General Linear Models (GLM) with temporal series projections until 2030 by the Expert Modeler Methods available on IBM SPSS Statistics v. 22 software (SPSS Inc. Chicago, IL, USA).

2.2. Salience Analysis

The scientific relevance of the selected papers identifying AdVs and HSVs in bats was estimated based on the attention that they received and according to a search that we conducted in February 2023 using Altmetric Explorer, a web-based platform available through 'Altmetric.com'. This platform provides the Altmetric Attention Score (ASS), which represents the attention that each paper receives through online media sources such as policy documents, news, YouTube, patents, peer reviews, and citations [18]. Additionally, we collected citation counts and scores by categories: (1) all papers published in the same year and journal, (2) all papers published in the same year, (3) all papers published in the same journal, and (4) all research outputs scored by Altmetric.com [19]. Furthermore, we correlated the ASS with the number of citations and the Journal Impact Factor (JIF) obtained from Altmetric.com, which are traditional bibliometric indicators for research, using the NCSS 12.0.9 software [19–21].

3. Results

The initial search yielded a set including a total of 2656 scientific papers focusing on AdVs and 1713 scientific papers focusing on HSVs. After removing duplicates and screening the papers according to the defined criteria, a total of 90 papers were included in the study. These papers were published between 1996 and 2022, with 55 papers that focused on AdVs (published between 2008 and 2022) and 54 papers focusing on HSVs (published between 1996 and 2021), with 19 articles for both viral types (Figure 1).

The review indicates that AdVs and HSVs have been studied in a total of 239 bat species worldwide, corresponding to 87 genera and 14 families (mostly, Vespertilionidae 37.2%, Pteropodidae 13.0%, and Phyllostomidae 10.9%). The majority of the bats included in the studies were relatively common bats that, in fact, are considered as "Least Concern" (LC) according to the conservation categories of the IUCN (Table S3).

3.1. Adenoviridae

During the selected period of time, the presence of AdVs was studied in 178 bat species, corresponding to 63 genera and 13 families. Most of the studied species belonged to the Vespertilionidae family (43.3%). There were also relevant studies on Pteropodidae (11.8%) and Rhinolophidae (11.8%) (Figure 2). The presence of AdVs in bats was confirmed in 29 countries, mainly in Asia (Figure 3), for a total of 97 species (54.5% of the total studied bat species) belonging to 42 genera and 11 families. The highest prevalence was detected in the family Vespertilionidae (46 out of the total 97 positive species), but also in Rhinolophidae (12 out of the 97 positive species) and Pteropodidae (12 out of the 97 positive species) (Figure 2; Table S4) [22–100].



Figure 2. Percentage of bat species by family tested for (**A**) adenoviruses and (**C**) herpesviruses and bat species positive for (**B**) adenoviruses and (**D**) herpesviruses for the time period 1996–2022.

Research is still completely missing in eight bat families (Cistugidae, Craseonycteridae, Furipteridae, Mormoopidae, Myzopodidae, Natalidae, Noctilionidae, and Thyropteridae). Although these families represent comparatively few species and most of them have a restricted distribution, it is important to complete their virological study. Furthermore, even within the studied families, the majority of their species remain unrepresented, as they have been investigated in less than 15% of their total diversity. Positive species for AdVs were found in all of the studied families except for Rhinopomatidae and Rhinonycteridae, due probably to their poor representation (Figure 4).

Still, our results showed a relevant matching between the distribution of the sampling efforts by family and the number of bats found to be positive for AdVs (Figure 2). In addition, there was a strong significant correlation between the number of species studied and species positive for each family (SC = 0.9050, p = 0.0000). Finally, the presence of AdVs relative to the family richness was evenly distributed across the whole order of Chiroptera (Figure 4).



Figure 3. Geographic location of the countries with positive bat species for AdVs (**above**) and HSVs (**below**). The color intensity indicates the number of positive species per country. In white are those countries where bats have not been assessed for AdVs and HSVs.





The highest number of AdV positive samples in a single bat species was found in the Indian flying fox *Pteropus medius* (n = 197) from Bangladesh, which represented around 10.4% of the 1092 samples inspected [65]. Similarly, 70 bent-wing bats of the species *Miniopterus natalensis* (around 25.5%) were positive out of 274 bats inspected in Kenya and South Africa [37,43], and 41 Gould's wattled bats *Chalinolobus gouldii* (17.7%) out 232 analyzed in Australia were positive [82]. Particularly, the species that exhibited a higher proportion of positive individuals in relation to the collected amount (excluding species with a collection of fewer than five individuals) were the leaf-nosed bat (*Doryrhina cyclops*), showing 15 positive out of 20 individuals from four localities in Cameroon [27], and the pipistrelle *Neoromicia tenuipinnis* had 5 positive individuals out of 11 collected at three different localities also in Cameroon [27], while the mouse bats *Myotis fimbriatus* had 19 positive bats out of 54 collected in various locations in China [88,91] (Table S5). It is important to be cautious with these last values due to the small sample size and the fact that they originated from particular collecting efforts and not from continuous monitoring over time and space.

All detected AdVs belonged to the genus *Mastadenovirus*. Most AdVs were identified in a single-host species; however, two viral types were identified in more than one bat species (Table 1), and in other instances, bats hosted different AdVs that presented high genetic similarity (\geq 95%). Examples include AdVs hosted by *Hypsugo savii* and *Pipistrellus kuhlii*; AdVs hosted by *P. kuhlii* and *P. pipistrellus*; or AdVs hosted by *Nyctalus noctula* and *N. lasiopterus*, *Eptesicus serotinus* and *Ia io*, *P. pipistrellus* and *N. noctula*, *Myotis macrodactylus* and *M. pilosus*, and *Myotis fimbriatus* and *M. myotis* [48,73,91,92].

Table 1. List of AdVs found in more than one bat species, indicating the name of the virus as referred to by the authors where it was initially identified, the host bat species, the country where they were collected, the number of positive bats for each virus, the identification method and the amplified gene, and the references.

AdVs	Bat Family	Bat Species	Country	Positive	Amplification PCR	Reference
Mastadenovirus	Vespertilionidae	Hypsugo savii	Spain	3	DNA Polymerase gene	[74]
	Vespertilionidae	Hypsugo savii	Italy	2	DNA Polymerase gene	[48]
	Vespertilionidae	Pipistrellus kuhlii	Italy	1	DNA Polymerase gene	[48]
Mastadenovirus Vespertilionid AdV-1	Vespertilionidae	Nyctalus noctula	Germany	4	DNA Polymerase gene	[73]
	Vespertilionidae	Myotis mystacinus	Germany	1	DNA Polymerase gene	[73]
	Vespertilionidae	Pipistrellus nathusii	Germany	1	DNA Polymerase gene	[73]

Sampling efforts were not geographically evenly distributed. The highest density of sampling localities was found in Europe, central Africa, and eastern Asia (Figure 3), whereas vast regions in all continents still stand out for the lack of studies on this matter, such as Canada in the Nearctic Region, north Africa, and the Middle East, all the way to central or northern Asia or even in Australia. The highest number of AdV-positive bat species was reported from China, with 30 positive species [23,26,28,32,40,78,79,88,91] out of 147 species reported for the country [101]. This vast country has shown an increasing interest in studying viruses in bats; in fact, the study on viruses hosted by bats is the bat topic most intensively studied in this country [101]. In Cameroon, there are 17 positive species [27] out of 58 reported species for the country [102,103], in Germany, 12 positive species [73,90,95,104] out of 24 reported for the country [105], and in Spain, 11 positive [74] out of 35 reported species [106] (Figure 3).

3.2. Herpesvirus

During the present study's time period, the presence of HSVs was investigated in 161 bat species corresponding to 63 genera and 11 families. Most of the studied species belonged to the family Vespertilionidae (37.9%), followed by the families Phyllostomidae

(16.1%), Pteropodidae (9.9%), and Rhinolophidae (9.9%) (Figure 2). The presence of HSVs was confirmed in bats from 34 countries, mainly in the Americas and Asia (Figure 3), for a total of 109 species, 45 genera, and 10 families of bats. The presence of HSVs was mainly detected in the families Vespertilionidae (45 out of the 109 positive species), Pteropodidae (16 out of the 109 positive species), and Phyllostomidae (14 out of the 109 positive species) (Figure 2; Table S3).

We found no information for ten bat families (Cistugidae, Craseonycteridae, Furipteridae, Megadermatidae, Mystacinidae, Myzopodidae, Natalidae, Noctilionidae, Rhinopomatidae, and Thyropteridae). Similar to the AdVs, a strong significant correlation was found between the total number of species studied and the species positive for HSVs within each bat family (SC = 0.9657, p = 0.0000). Although the bat families studied for HSVs appeared also underrepresented when we consider the total number of species within families. As a result, we detected a clear correspondence across families between the number of species positive for HSVs and the number of species investigated within each family (Figures 1 and 3). Positive species for HSVs were found in all of the studied families except for Nycteridae, due probably to their poor representation. On the contrary, all species of flying foxes (Pteropodidae) that have been studied (16 species) resulted in being positive for HSVs (Figure 4).

The highest number of HSV positive samples was documented in the Indian flying fox *Pteropus medius* in Bangladesh, with a total of 730 positive out of the 1741 samples examined and representing over 40% of the studied bat population [65]. Adding results from different samplings and regions, a total of 215 vampire bats (*Desmodus rotundus*) out of 338 sampled bats were found positive from an area covering Mexico, Guatemala, Peru, French Guiana, and Uruguay [25,44,45,51,52,107], and 89 Australasian bent-wing bats (*Miniopterus orianae*) were positive out of 467 bats studied from Australia [38].

Similarly, the species that exhibited a higher proportion of positive samples (excluding those species represented by five or less individuals) were the Madagascar fruit bat *Eidolon dupreanum*, with all individuals tested (9) being positive [55], the free-tailed bat *Tadarida brasiliensis*, with 25 positive out of 28 bats studied in Uruguay [44], and the European free-tailed bat *Tadarida teniotis*, with 6 positive bats out of 7 tested in Spain [39] (Table S4). Similar to the AdVs, the presence of HSVs showed a wide variation among bat families or geographical regions but without presenting clear patterns. In addition, it is important to keep in mind that the reported positive data come from individuals collected generally at the same locality or from close localities and at the same time. Therefore, these data reflect poorly the real prevalence of AdVs and HSVs across entire populations or species.

The detected HSVs belonged to the subfamilies Alphaherpesvirus, Betaherpesvirus, and Gammaherpesvirus, including the genera *Varicellovirus, Simplexvirus, Cytomegalovirus, Muromegalovirus, Proboscivirus, Roseolovirus, Lymphocryptovirus, Percavirus, Rhadinovirus,* and *Macavirus*.

Seven HSVs were identified in different bat species, and some HSVs were even shared between bats and other mammals, as in the case of the *Gammaherpesvirus murino* 68 (MHV-68). This virus was originally isolated from free-living rodents in Slovakia and was later detected by PCR in a blood sample of the common noctule (*Nyctalus noctula*) in Ukraine [81]. Moreover, other bats (four *Myotis blythii* and one *Barbastella barbastella*) showed antibodies against MHV-68 in Slovakia [81], and a closely related virus was found in a liver of the lesser long-nosed bat (*Leptonycteris yerbabuenae*) in Mexico [54] (Table 2).

The largest number of positive species for HSVs was reported from China, where 33 bats tested positive [26,32,42,75,78,91,108] out of the 147 species reported for the country [101]. A total of 24 species were found positive [39] out of the 35 reported for Spain [106], 9 species were found positive [45,53] out of 106 reported for French Guyana [109], and in Germany, 9 species were found positive [87,90,94] out of the 24 bats reported for the country [105] (Figure 3).

Table 2. List of HSVs found in more than one bat species, indicating the name of the virus as referred to by the authors, the host bat species, the country where they were collected, the number of positive bats for each virus, the identification method used and the amplified gene, and the respective references. * Difference in a single nucleotide.

HSVs	Bat Family	Bat Species	Country	Positive	Identification Technique	References
Gammaherpesvirinae <i>Rhadinovirus</i> BatGHV-1	Vespertilionidae	Eptesicus serotinus	Germany	2	PCR (Glycoprotein B and DPOL gene)	[87,94]
	Vespertilionidae	Myotis nattereri	Germany	1	PCR (Glycoprotein B and DPOL gene)	[94]
	Vespertilionidae	Pipistrellus nathusii	Germany	1	PCR (Glycoprotein B and DPOL gene)	[94]
	Vespertilionidae	Pipistrellus pipistrellus	Germany	2	PCR (Glycoprotein B and DPOL gene)	[94]
Gammaherpesvirinae <i>Rhadinovirus</i> BatGHV-2	Vespertilionidae	Myotis nattereri	Germany	2	PCR (DPOL gene)	[94]
	Vespertilionidae	Myotis myotis	Germany	1	PCR (DPOL gene)	[94]
Gammaherpesvirinae <i>Rhadinovirus</i> BatGHV-3	Vespertilionidae	Nyctalus noctula	Germany	8	PCR (DPOL gene)	[87,94]
	Vespertilionidae	Myotis nattereri	Germany	1	PCR (DPOL gene)	[94]
	Vespertilionidae	Myotis myotis	Germany	1	PCR (DPOL gene)	[94]
Gammaherpesvirinae <i>Rhadinovirus</i> BatGHV-4	Vespertilionidae	Nyctalus noctula	Germany	2	PCR (Glycoprotein B and DPOL gene)	[94]
	Vespertilionidae	Myotis nattereri	Germany	1	PCR (Glycoprotein B and DPOL gene)	[94]
	Vespertilionidae	Pipistrellus nathusii	Germany	9	PCR (Glycoprotein B and DPOL gene)	[87,94]
Gammaherpesvirinae	Vespertilionidae	Nyctalus noctula	Germany	1	PCR (DPOL gene)	[87]
BatGHV-5	Vespertilionidae	Myotis myotis	Germany	1	PCR (DPOL gene)	[87]
	Vespertilionidae	Myotis mystacinus	Germany	1	PCR (DPOL gene)	[87]
Betaherpesvirinae BatBHV-1	Vespertilionidae	Myotis nattereri	Germany	3	PCR (DPOL gene)	[94]
	Vespertilionidae	Pipistrellus pipistrellus	Germany	2	PCR (DPOL gene)	[94]
	Vespertilionidae	Myotis blythii	Slovakia	4	Virus-neutralizing antibodies	[81]
Gammaherpesvirinae <i>Rhadinovirus</i>	Vespertilionidae	Barbastella barbastella	Slovakia	1	Virus-neutralizing antibodies	[81]
MHV-68	Vespertilionidae	Nyctalus noctula	Ukraine	1	PCR (ORF50 gene)	[81]
	Phyllostomidae	Leptonycteris yerbabuenae *	Mexico	1	PCR (ORF50 gene)	[54]

3.3. Published Research of Adenoviridae and Herpesviridae in Bats

The papers analyzed in this study were mainly published in international scientific journals such as *Viruses* (13.2%), *PLoS ONE* (11%), and *Journal of Virology* (9.9%), with a focus on viral identification (70.3%) and viral diversity (6.6%).

This review has revealed that the studies on AdVs or HSVs in bats were primarily conducted by researchers from Asia (35.6%), especially from China, with a total of 16 published papers, followed by Europe (27.8%) and America (23.3%) (Figure S1). There was a strong significant correlation between the number of species positive for both AdVs and HSVs families and the number of species studied in each country (AdVs SC = 0.9582, p = 0.0000; HSVs SC = 0.9482, p = 0.0000). In relation to the methodology applied, most studies used molecular methods that proved to be very effective in detecting viruses of these families and followed to a lesser extent by serological tests, such as enzyme-linked immunosorbent assay (ELISA) and virus neutralization test.

The analyzed studies in this survey were focused on case studies from areas in all continents, with a total of 44 countries, mainly from China (14.4% of papers), the United States of America (7.8%), and Japan (7.8%), whereas south American and African countries have very few research teams focusing on AdVs and/or HSVs in bats (Figure 3). The bipartite space association network showed geographical proximity between case studies and research teams in Asia, Europe, and Oceania. Studies in South America were conducted mainly by researchers from Scotland and the United States, while African bats have been addressed mainly by researchers from England, the United States, and Japan. On the other hand, researchers from the USA and China have diversified their studies, covering many countries (Figure 5). The temporal evolution of the number of AdV and HSV publications has changed widely over time, with very few studies dating before 2011, and no publications from 1997 to 2006, the years of the descriptions of the first bat Herpesvirus and the first bat Adenovirus, respectively. The variations in publications are apparently not related to any epidemic or pandemic events reported by the World Health Organization, as Figure 6 shows.



Figure 5. Spatial networks of study sites (green circles) and research teams (blue circles). The sizes of the circles reflect the number of studies of a specific site, and the arrows represent the direction from the research team to the study site, while the line width represents the number of papers published by each research team.



Figure 6. Number of published papers per year, including projections of the number of publications from 2023 to 2030, according to the Expert Modeler Method, indicating the Upper Control Limit (UCL) and Lower Control Limit (LCL). In addition, the figure highlights some epidemic/pandemic events reported by the World Health Organization.

The publication trend shows a clear increasing trajectory, with a predicted annual publication rate of 14 papers per year for 2030, according to the projections based on the current publication time series (Figure 6).

3.4. Bibliometric Analysis

Attention scores were extracted from a total of 91 papers, with 15 papers being excluded as they were not evaluated by Altmetric Explorer, possibly due to the lack of direct links to the publications or because they presented citation metadata incompatible with Bookmarklet of Altmetric. The higher AAS values were observed in papers published in the journals *MBio, Journal of Virology*, and *ISME Journal*. A positive correlation was found between the Altmetric score and the number of citations (SC = 0.3649, *p* = 0.0018) as well as the impact factor (SC = 0.3302, *p* = 0.0041), indicating a significant interest for this subject by the scientific community. Although some studies have received little attention, more than half of the papers were ranked in the top 25% of the most cited and commented papers worldwide (Figure S2).

4. Discussion

The importance of bats as natural reservoirs of viruses of potentially emerging diseases has increased in recent times since several of the last viral zoonoses transmitted to humans and therefore of global health concern—were found to be directly or indirectly related to bats. Indeed, bats serve as natural hosts for numerous viruses, including rhabdoviruses, paramyxoviruses like Hendra and Nipah viruses, coronaviruses, and filoviruses. Most of these viruses can potentially cause illness in both domestic animals and humans, and this fact has substantiated a widespread concern about the role played by bats in the context of a one health framework [110].

Adenoviruses (AdVs) and herpesviruses (HSVs) are two highly diversified groups of double-stranded DNA viruses that can infect numerous vertebrate species and are considered of clinical interest [5,11]. It is known that these viruses are commonly hosted by bats; therefore, it is important to summarize the advances that have taken place recently for a better understanding of the ecological and evolutionary relationships between bats and their viruses and to explore the direction in which these recent research efforts should point in the future. In this context, we have conducted the first bibliographic review of the adenoviruses and herpesviruses found in bats. The aims of this study were to analyze the bat species known to host AdVs and HSVs worldwide, to describe their distribution, and to contribute to the understanding of the role played by bats as hosts for these two large viral families. This review fills in an existing gap and completes the information already gathered at different scales on other viral families such as Coronaviridae [111–115], Retroviridae [116], Rhabdoviridae [114], and Paramyxoviridae [117].

The first AdV in a bat was obtained from an isolate from the Ryukyu flying fox (*Pteropus dasymallus yayeyamae*) from Japan in 2008 using the Polymerase Chain Reaction (PCR) method and named Ryukyu virus 1 (RV1) [63]. Since then, numerous AdVs have been identified in a total of 97 bat species in 11 families.

Similar phylogenetic relationships have been reported between the AdVs found on European bats and their hosts [74]. In a study of the association between life traits of the bats and their probability of hosting adenoviruses, a positive association was found with bats' mating strategy [118]. This study also suggested that the prevalence varied largely across species and localities and that—at least for some species—males were more likely to be infected by AdVs than females [118].

Despite a general species specificity, several studies have reported the presence of the same AdVs or closely related viruses (>95% identity) from bats belonging to different families and even from different geographical regions [48,73,91,92]. Remarkably, high genetic identity (>97%) was also reported between AdVs found in bats and AdVs found in rats and shrews [65,88,119].

The data suggest the potential capacity of these AdVs to infect different bat species and cross species barriers, and in fact, host switching is well known for the family, supported by phylogenetic and serological evidence between AdVs from different [120,121]. Nonetheless, it is crucial to approach this information with caution and account for factors such as host species identification, especially for cryptic species, as well as the mutation rate and the size of the amplified fragment used when comparing viruses across different hosts.

The mechanisms by which these AdVs could cross from their hosts to other species remain unclear. It is speculated that such events could take advantage of shared water sources, such as ponds or rivers where humans, livestock, domestic animals, and wildlife may represent potential sources of exposure [110,120]. These environments could serve as mixing points, facilitating viral transmission between different species. However, further research is needed to fully understand the dynamics and pathways involved in the potential cross-species transmission of AdVs.

The first isolation of a bat-associated herpesvirus was obtained from the submandibular gland tissues of the little brown myotis (*Myotis lucifugus*) in the USA in 1996, using electron microscopy [93]. Since then, and until 2022, a total of 109 bat species in 10 families have been identified as hosts for HSVs.

In the present study, specific HSVs were identified for most of the bat species studied. These findings support the idea of general parallel evolution between the HSVs and their bat hosts, as suggested recently [39]. In this study on the HSVs of Iberian bats, a remarkable concordance was found between the phylogeny of the viruses and the phylogeny of their bat hosts [39], and distinct but related HSVs were found infecting each of two morphologically cryptic and highly sympatric Iberian *Myotis (M. crypticus* and *M. escalerai*) species [39].

In our review, we also identified certain HSVs that were shared among multiple species (Table 2). It is important to underline that the bats were identified in the majority of these studies both morphologically and genetically, ensuring a trustable species identification. The presence of HSVs in more than one species suggests that despite the typical specificity exhibited by HSVs, bat hosts and their viruses could have shared a common evolutionary history in specific situations. However, it is of paramount importance to rigorously confirm the presence of presumably the same virus in more than one host species, since this is not clear in some cases.

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Some HSVs found in bats have experimentally shown the ability to infect and replicate in human, monkey, feline, and swine cell lines [54,57,64,85], indicating the potentiality of infecting other mammals. On the other hand, metagenomic studies have reported the presence of human herpesviruses in bats from Croatia, China, and Mexico [41,56,91]. However, metagenomics results could originate easily from either similar viruses or from contamination during the lab processing, and given the high sensitivity of the technique, we need to be cautious in the interpretation of these results.

Comparison of the number of positive bat species for AdVs (97) and HSVs (109) with other viral families is challenging due to the fact that the majority of previous studies have focused on specific regions [111–114,122,123], conducted analyses only at the bat family level [124], or solely considered viral sequences uploaded to databases [125]. However, the number of positive species in this review is the most extensive reported for any viral family previously. Among the few comparable analyses, a study [126] reports 75 bat species positive for the family Flaviviridae, although this study does not encompass all flaviviruses genera. Another study [116] has documented 51 positive bat species for viruses of the family Retroviridae.

A study limited to Europe reported a high number of bat species testing positive for Adenoviridae (23 species), Herpesviridae (27 species), and Coronaviridae (29 species) [114]. Similarly, high numbers of positive bats species are reported in the Americas [112] for the family Coronaviridae (42 species); and only for Brazil, 26 bats are reported positive for Coronaviridae, 24 species for Herpesviridae, and 53 bat species for Rhabdoviridae [123]. In Africa, high numbers of positive bat species are reported for Coronaviridae (59 species) and Filoviridae (12 species) [113,122]. Finally, 31 bat species were found to be positive for Coronaviridae in Australia [111].

Despite the variation in coverage in the surveyed studies, the proportion of bat species that are positive for AdVs and HSVs is strongly correlated to the number of species that have been studied for each country. In other words, in general, and for any locality, the more species studied, the greater number of species positive for AdVs and HSVs found. For example, Indonesia, which holds the highest bat diversity in the world, with 221 species [101], has not studied bats for AdVs, although the three species of bats tested for HSVs resulted in being positive [57,58]. Colombia and Ecuador, the second and fourth most diverse countries in the world with 187 and 171 species of bats, respectively [101], have not studied AdVs and HSVs in bats so far. While, in Brazil, the third most diverse country, with 183 species [101], only one species was found to be positive for AdVs and two species positive for HSVs [50,55,127]. These data give an idea of how incomplete remains our present knowledge for the majority of regions, and of how much sampling is still needed, especially in areas with expected high potential for virus diversity owing to their rich diversity of bats.

The majority of the bats studied that are hosting either AdVs and/or HSVs seem to be abundant and considered "Least Concern" (LC) according to the IUCN red list, which combines data on population sizes and geographic range area (Table S4). This result probably indicates that in general, the samplings are biased toward the most common species for the different areas. Contrary to our results, a study points out that bats included within the categories Near Threatened (NT) and Vulnerable (VU) of the IUCN showed higher mean viral richness than bats considered as LC, suggesting that NT and VU species are more susceptible to viral infection [127]. Although these results warrant caution given the uneven and limited sampling of the paper, it seems that more specific studies are needed to clarify the relation between abundance and virus prevalence in bats.

The total number of bats studied for AdVs and HSVs (238 species) represent only about 17% of the worldwide bat diversity [128]. Most of these species belong to the families Vespertilionidae, Rhinoliphidae, Pteropodidaae, and Phyllostomidae, which all include a high diversity of bats and present wide distribution. As a consequence, these families also present more positive species for AdVs and HSVs than other bats, similarly as it was found in other viral families like Coronaviridae, Paramyxoviridae, Astroviridae, Rhabdoviridae,

Flavoviridae, and Polyomaviridae [12,124,125]. This fact may be related to a bias in interest, receiving more attention than those species of bats considered to have more chance to be natural reservoirs of emerging pathogens, such as Hendra, Nipah, Ebola, Lyssavirus, SARS or MERS coronaviruses [129–131]. Other factors to consider are the differences in bat life traits (e.g., migrating behavior, roosting habits, etc.), differences in their availability, or even differences between countries in the levels of bat protection. In any case, this review has evidenced the present lack of knowledge regarding the presence of both viral families in several bat families such as Craseonycteridae, Myzopodidae, Noctilionidae, Furipteridae, Thyropteridae, Natalidae, and Cistugidae. This knowledge is almost anecdotical for other bat families such as Mormoopidae, Rhinopomatidae, Megadermatidae, and Mystacinidae. Most of these families have a very limited distribution, are only represented by a few species, and/or are rare, thus hindering their study. Still, future studies should focus on them.

The number of articles included in the present study is small compared to other studies on other groups of viruses. Most of the bat viruses isolated by metagenomics NGS and reported in NCBI/GenBank correspond to RNA viruses (85.8%), mainly coronavirus (30.74%), rhabdovirus (24.28%), and paramyxovirus (9.97%). These differences are the result of a bias in the surveillance of certain viral families that may represent a higher zoonotic risk [122,124,129,131].

The importance of gathering basic information is supported by the fact that the large majority of the papers (70.3%) focus mostly on viral identification and description, which is essential for understanding global viral diversity. To be acquainted of this viral diversity is crucial for developing specific diagnostic methodologies to identify possible risks among AdVs and HSVs, keeping in mind that some of them can potentially have worrisome consequences on human health or domestic animals [101].

Regarding geographical patterns, the results of our screening indicate that despite a relatively wide coverage across continents in the study of AdVs and HSVs in bats, there are still quite important areas that have not been studied yet. In fact, there are many regions, particularly in central America, north Africa, west Asia, central Asia, north Asia, and Australasia, in which the search for AdVs and HSVs in bats was so far scarce or never carried out. This finding is quite surprising for some areas that are located in countries considered developed and indicates how far we still are from having gathered the basic information needed for the designing of future general antiviral strategies. The weakness in the sampling areas worldwide is followed by the lack of local research teams capable of carrying out studies aimed to detect not only adenoviruses or herpesviruses but also other viral families hosted by bats [131]. The most important research teams belong to US and Chinese institutions, followed by European researchers. This study points to the necessity of fostering local capacity for many countries in order to be able to establish efficient surveillance networks worldwide.

The scientific interest in the detection of AdVs and HSVs has shown also a strong variation over time, showing an important increase in the last decade, probably in response to a variety of factors that would include the growing interest in viral diversity [12,125,132] together with the decrease in costs associated with molecular detection, given that the vast majority of the papers included in this study used either PCR detection or metagenomics. Finally, the increase in general interest in the diversity of bat-hosted viruses results also from the fact that some of the recent emerging infectious diseases caused by viruses seem to be related to bats, either as natural reservoirs or as hosts of related viruses [133,134].

The impact of scientific advances on our society is often difficult to quantify. By using algorithms, such as those employed by altmetic.com, we were able to evaluate the online impact of published articles and take into consideration the social interactions of scientists and the public in general. In this study, the 'attention score' (AAS) presented correlations with all of the traditional bibliometric indicators, such as the citation count or the JIF [20]. Still, we consider that is important to include in reviewing studies like this algorithms like the AAS, which should be seen as a complement and not as an alternative

to traditional bibliometric indicators. The results of our review support a growing interest within the research community in relation to bats as potential reservoirs for viruses, as a significant portion of the published articles rank among the most widely read, discussed, and cited papers globally today. Nevertheless, it is important to be careful when addressing this scientific interest in such a way as to avoid undesirable misconceptions and negative effects on the public perception of bats. This negative impact has increased dramatically and in an unjustified manner after the recent pandemic and has provoked worrisome direct consequences on the conservation of bats despite their fundamental ecosystem services [135,136].

Supplementary Materials: The following supporting information can be downloaded at: https: //www.mdpi.com/article/10.3390/d16010046/s1, Table S1: Search engines and keywords used. Table S2: Data extracted from each article that was included in the review. Table S3: Conservation status by IUCN red list category of the bat species. Table S4: Bat species positive for adenoviruses (AdVs) and/or herpesviruses (HSVs), indicated by a dark box and information about the conservation category of species in the IUCN, the country where it was found, and the corresponding reference. Table S5: Prevalence of AdVs and HSVs by species, including only those articles where the sample size and the number of individuals positive for AdVs and/or HSVs are reported, type of sample analyzed for each viral type, sample size (n), number of positive species (positive), and prevalence (P%). Figure S1: Continents of origin of research teams that have studied AdVs and HSVs in bats. Figure S2: Violin plots representing A. all research outputs scored by Altmetric.com, B. all papers of the same journal, C. all papers of the same year, and D. all papers of the same year and journal. Standardized ranking position is represented between 0 (first position) to 100 (last position).

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