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REVIEW

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Bat Viral Shedding: A Review of Seasonal Patterns and Risk Factors

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Abstract

Background: Bats act as reservoirs for a variety of zoonotic viruses, sometimes leading to spillover into humans and potential risks of global transmission. Viral shedding from bats is an essential prerequisite to bat-to-human viral transmission and understanding the timing and intensity of viral shedding from bats is critical to mitigate spillover risks. However, there are limited investigations on bats' seasonal viral shedding patterns and their related risk factors. We conducted a comprehensive review of longitudinal studies on bat viruses with spillover potential to synthesize patterns of seasonal viral shedding and explore associated risk factors.
Methods: We extracted data from 60 reviewed articles and obtained 1085 longitudinal sampling events. We analyzed viral shedding events using entropy values to quantitatively assess whether they occur in a consistent, pulsed pattern in a given season.
Results: We found that clear seasonal shedding patterns were common in bats. Eight out of seventeen species-level analyses presented clear seasonal patterns. Viral shedding pulses often coincide with bats' life cycles, especially in weaning and parturition seasons. Juvenile bats with waning maternal antibodies, pregnant bats undergoing immunity changes, and hibernation periods with decreased immune responses could be potential risk factors influencing seasonal shedding patterns.
Conclusion: Based on our findings, we recommend future longitudinal studies on bat viruses that combine direct viral testing and serological testing, prioritize longitudinal research following young bats throughout their developmental stages, and broaden the geographical range of longitudinal studies on bat viruses based on current surveillance reports. Our review identified critical periods with heightened viral shedding for some viruses in bat species, which would help promote efforts to minimize spillovers and prevent outbreaks.

Keywords: bat-borne viruses, viral shedding, seasonal patterns, spillover risk

Introduction

Throughout history, various zoonotic viruses have spilled over into humans, including HIV from primates, influenza A virus from birds, and SARS-CoV-2, suspected to originate from bats (Sharp and Hahn, 2011; Liu et al., 2013; Zhou et al., 2021). Bats are important natural reservoirs for numerous zoonotic viruses, including rabies, Marburg, Nipah, and others, which cause high mortality in cases and can lead to severe outbreaks (da Rosa et al., 2006; Dovih et al., 2019; Plowright et al., 2019). Despite their association with diseases, bats provide essential ecosystem services such as pest control, pollination, and seed dispersal, crucial for environmental and agricultural health (Kunz et al., 2011; Rocha et al., 2021). This double-edged influence of bats highlights the necessity of a balanced perspective that fosters strategies to safeguard both human health and bats' ecological contributions.

Our understanding of the mechanism of bat-to-human viral transmission is limited for many viruses. However, a key step in this process is overcoming several ecological barriers to cross-species transmission, one of which is the timing and intensity of viral shedding from the reservoir host (Plowright et al., 2017). Viral shedding from bats provides the source of infection. Interactions between humans and bats, such as habitat encroachment or wildlife trade, bring people into proximity

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with these infectious agents (Shivaprakash et al., 2021; Eby et al., 2023). When these human activities are aligned with bat viral shedding events, these circumstances can bridge the gap for zoonotic spillover. Recognizing the importance of viral shedding in zoonotic spillover, pinpointing risk factors of shedding intensity and frequency could inform public health strategies to reduce potential transmission. Previous research has identified various factors that might influence viral shedding in bats, including physiological states like pregnancy, stress, and neonatal immunity, and extrinsic elements such as climatic conditions and food resources (Seltmann et al., 2017). However, these studies are usually restricted to a narrow scope, focusing on specific viruses, bat species, and regions. A broader understanding of the seasonal viral shedding patterns from bats would improve our understanding of zoonotic virus dynamics and promote more effective preventive measures during critical periods.

This review comprehensively synthesized existing longitudinal studies on viral shedding from bats, focusing on viral families associated with spillover into humans that have been longitudinally studied, including *Coronaviridae*, *Lyssaviridae*, *Paramyxoviridae*, *Astroviridae*, and *Filoviridae*. We aim to determine any discernible seasonal shedding patterns across different viruses within bat populations and to identify risk factors that could influence these dynamics.

Methods

Search strategies and selection criteria

To identify longitudinal viral studies on wild bats, we followed the PRISMA protocol (Moher et al., 2009). The search strategy for this review targeted a selected group of virus families and genera: *Coronaviridae*, *Paramyxoviridae*, *Rhabdoviridae (Lyssavirus), Filoviridae*, *Reoviridae* (*Orthoreovirus*), *Astroviridae*, *Flaviviridae* (*Hepacivirus*), and *Hantaviridae*. These taxa are commonly present in bats and, for some viruses, have considerable implications for zoonotic spillover and human health impact (Wang and Anderson, 2019; Letko et al., 2020). Our search terms paired virus family names with "bat" and "seasonal/longitudinal." A systematic search was conducted on May 15, 2023, across four databases: PubMed Central (PMC), Scopus, Web of Science, and Google Scholar (Supplementary Table S1). We further cross-referenced with other comprehensive reviews on bat viruses and integrated any pertinent studies into our full-text review (Becker et al., 2019; Plowright et al., 2019; Kessler et al., 2018; Crowley et al., 2020; Olival and Hayman, 2014; Ruiz-Aravena et al., 2022; Cohen et al., 2023).

Both authors evaluated papers independently using the Covidence platform, with any conflicts resolved by consensus. Inclusion criteria specified studies that conducted longitudinal sampling on bats from the same location at least three times, with PCR or serological testing for at least one targeted virus. We excluded studies that did not collect samples from wild bats, thus excluding research on captive populations. Studies were also excluded if they did not offer specific temporal data, lacked original data, non-English articles, or had inaccessible full texts. Preprints were included if they had no corresponding published version, ensuring the inclusion of the broadest possible dataset.

Data analysis

Data extraction and data cleaning. In data extraction, our review collected the following information from each study: publication details (title, author, and DOI), virus family (and genus/species, if specified), bat species, and geographical information. We also extracted sample information, including sample type and testing method, sampling period, sample size, and the number or proportion of positive samples.

We defined a sampling event as one or multiple samplings conducted in the same geographic location and tested the same virus from each study, all carried out within 1 week. We selected the dominant sample type for each virus used for direct viral testing (*e.g.,* PCR tests) or serological testing if there were duplicated testing of the same bat, such as urine for henipaviruses and feces for coronaviruses (Baker et al., 2012; Olival and Hayman, 2014; Fischer et al., 2017; Peel et al., 2019; Cohen et al., 2023). To avoid bias from small sample sizes, we excluded events with less than ten bats sampled. After deleting duplicated events and filtering sample size, we retained records with at least three events at the same location for robust longitudinal analysis. For each unique event, we calculated its positive ratio (prevalence and seroprevalence), which was the proportion of samples with detected RNA or antibodies against the virus. Prevalence data, especially from fecal, oral, and urine samples, provided information about active viral shedding. Seroprevalence indicates levels of antibodies acquired postinfection or reflects the dynamics of immunity from maternal antibodies (Sohayati et al., 2011). Although serostatus does not directly reveal infections and viral shedding, variations in seroprevalence still inform the antibody dynamics and provide insights into potential infection and viral shedding (Hayman, 2015). Additionally, serological testing is a safer and more practical alternative for assessing infections for some viruses, like filoviruses and lyssaviruses (Plowright et al., 2015; Leendertz et al., 2016). Notably, most serological studies tested the overall level of antibodies against the virus in bats instead of specifying their IgG or IgM (Robardet et al., 2017; Boardman et al., 2020).

Statistical analysis. Many intrinsic and extrinsic factors impact seasonal patterns of viral shedding, like the climate and bats' biological characteristics (Montecino-Latorre et al., 2020; Eby et al., 2023). Pooling data from diverse environments and species might obscure the original seasonal patterns. Hence, we grouped studies based on their viruses, continents, and bat species and selected examples for species-level analysis, according to our inclusion criteria. Included studies must have at least four nonconsecutive timepoints of sampling, each of which replicated in at least one subsequent calendar year within a calendar month. The threshold spanning four timepoints (months) could cross at least two different seasons, providing a broad temporal context to identify evidence for seasonal patterns (Supplementary Fig. S1). While a threshold with more timepoints could potentially identify seasonal trends more clearly, it might exclude valuable data. Additionally, we required every timepoint to have at least one repeated sampling across different years to avoid opportunistic high or low prevalence. Our included examples had events from similar ecological regions since bat species are relatively locally grouped, justifying their collective analysis (Maganga et al., 2014). The furthest events within one example are filoviruses detected in *Rousettus aegyptiacus* from Zambia and South Africa, separated by 1485 km. Furthermore, we sourced life cycle information for bat

populations within these examples from the original studies or additional publications, including mating, parturition, weaning, and hibernation periods, if applicable.

We used entropy to quantify the variance in positive ratios across one year (Hurme et al., 2022). Higher entropy values suggest a significant concentration of virus shedding or seropositivity at a given time of the year, while lower values indicate a more uniform distribution. To calculate entropy, we first calculated the monthly average positive ratio (P_m) within each example, and then summed them, $P_t = \sum_1^{N_{mon}} P_m$, where N_{mon} is the number of months with collected data. The yearly entropy (E) against a uniform distribution $\left(q_m = \frac{1}{N_{mon}}\right)$ was calculated with $E = \sum_1^{N_{mon}} \left[\frac{P_m}{P_t} * log_2\left(\frac{P_m}{P_t}/q_m\right)\right]$. We analyzed two hypothetical datasets to assess the utility and the range of entropy values in identifying seasonality. The first dataset had 100% prevalence in a single month and 0% in the remaining 11 months, representing an extreme seasonal distribution. The second dataset had a 50% prevalence across all 12 months, representing a consistent distribution without any seasonality. The former dataset yielded an entropy value of 3.58, and the latter resulted in an entropy value of 0.00. Therefore, we interpreted the entropy values derived from our later empirical data within this defined range, where 0.00 denotes a uniform distribution, and 3.58 reflects pronounced seasonal variation (Supplementary Fig. S2). We assessed the average and concentration of E in each example with means (μ_E) and coefficients of variance (CV_E). Finally, we used the median of E and the mean of CV_E from all examples to represent their average levels.

To identify clear seasonal patterns, we combined quantitative entropy values with visually observed seasonal distributions. We depicted the yearly seasonal distributions and averaged them, weighted by sample sizes, to illustrate their average distributions for each example. We defined the highest peaks as the absolute peak in yearly distributions and as the average peak in average distributions. Combining two quantitative measures (μ_E and CV_E) and two highest peaks, we considered a particular bat species and virus combination to have clear seasonal patterns if $\mu_E \geq median(E)$, $CV_E \leq mean(CV_E)$, and the absolute and average peaks were distributed within the same or adjacent months.

Results

Database overview

Our review identified 60 publications eligible for data analysis from 2074 articles obtained after searching (Supplementary Dataand Fig. 1). The 60 included publications contributed 1622 sampling events targeting various bat viruses. After data cleaning, we obtained 811 longitudinal events for serological studies and 274 for viral detection studies (Table 1).

Direct viral testing had lower positive ratios compared to serological testing for the same virus (Supplementary Table S2). The average seroprevalence observed, especially in Hendra and Hendra-related viruses (49.3%) and filoviruses (30.7%), were significantly higher compared to their prevalence of 3.6% and 2.5%, respectively. The minor distinction observed between the viral (17.3%) and serological (25.2%) testing for lyssaviruses might be because of the low seroprevalence reported in one study with a large sample size (DL Horton et al., 2020). Excluding this outlier, the average seroprevalence for lyssaviruses was 33.0%, reinforcing the trend of higher values from serological assays. This pattern was consistent with the nature of serological testing, which suggested historical exposure instead of the current infection landscape. Conversely, astroviruses, coronaviruses, and paramyxoviruses were confined to direct viral testing, with average prevalence of 11.5%, 16.7%, and 8.1%, respectively. Among all tests, lyssaviruses, coronaviruses, and astroviruses had the highest prevalence, potentially implying more active shedding of these virus families.

The geographical distribution of longitudinal studies on bats exhibited distinct patterns across virus families (Supplementary Table S2). Some viruses, such as Hendra virus in Australia and Nipah virus in Asia, demonstrated region-specific distribution because of their actual region-limited presence (Liu et al., 2024). Some viruses, like coronaviruses and lyssaviruses, exhibited a broad dispersion across multiple continents in longitudinal studies due to their actual global distribution (Banyard et al., 2014; Olival et al., 2017; Becker et al., 2021). However, longitudinal data on filoviruses and paramyxoviruses were predominantly reported in Africa, which is narrower than their reported detection (XL Yang et al., 2017). Notably, within Africa, all detections using Nipah, Hendra, and Cedar antigens were identified as their related viruses or henipaviruses through serological assays rather than as the specific pathogenic entities themselves (Brook et al., 2019). This implies the presence of antigenically similar viruses, possibly new henipaviruses or paramyxoviruses as mentioned in other studies, that trigger cross-reactive responses in serological assays (Drexler et al., 2009, 2012; Madera et al., 2022).

Seasonal patterns at the species level

We included 17 eligible examples for species-level analysis, each focusing on one virus family in a bat species within one continent and summarizing data from one to several articles (Supplementary Table S3). All bat species included in the 17 examples focus on bat species that act as reservoirs for the related viruses, which are often the main source of viral shedding. These species vary in behaviors and diet (Supplementary Table S4): 7 out of 12 bat species are frugivorous, which may lead to more overlap with human food resources (Ramanantsalama et al., 2022). Three of these species exhibit hibernation behavior, while the others do not.

We assessed seasonal patterns of included examples with μ_E, CV_E, and the consistency of positive ratio peaks (Table 2). After aligning seasonal peaks, we compared μ_E and CV_E to their average levels across all examples. Bat-virus combinations with μ_E above the median entropy ($median(E) = 0.88$) and CV_E below the average ($mean(CV_E) = 0.74$) for viral detections were considered to have clear seasonal patterns. For serological testing, μ_E above the median ($median(E) = 0.08$) and CV_E below the average ($mean(CV_E) = 1.01$) were also considered evidence of clear seasonality. Eight bat-virus combinations displayed clear seasonal patterns out of 17 eligible examples; four were from Africa, two from Asia, and another two from Europe (Table 2 and Fig. 2).

Examples with clear seasonal patterns. Direct detection of astroviruses in *Mormopterus francoismoutoui* from Réunion resulted in μ_E of 1.18 and CV_E of 0.27. The μ_E exceeded 0.88 and CV_E was much lower than 0.74, indicating the

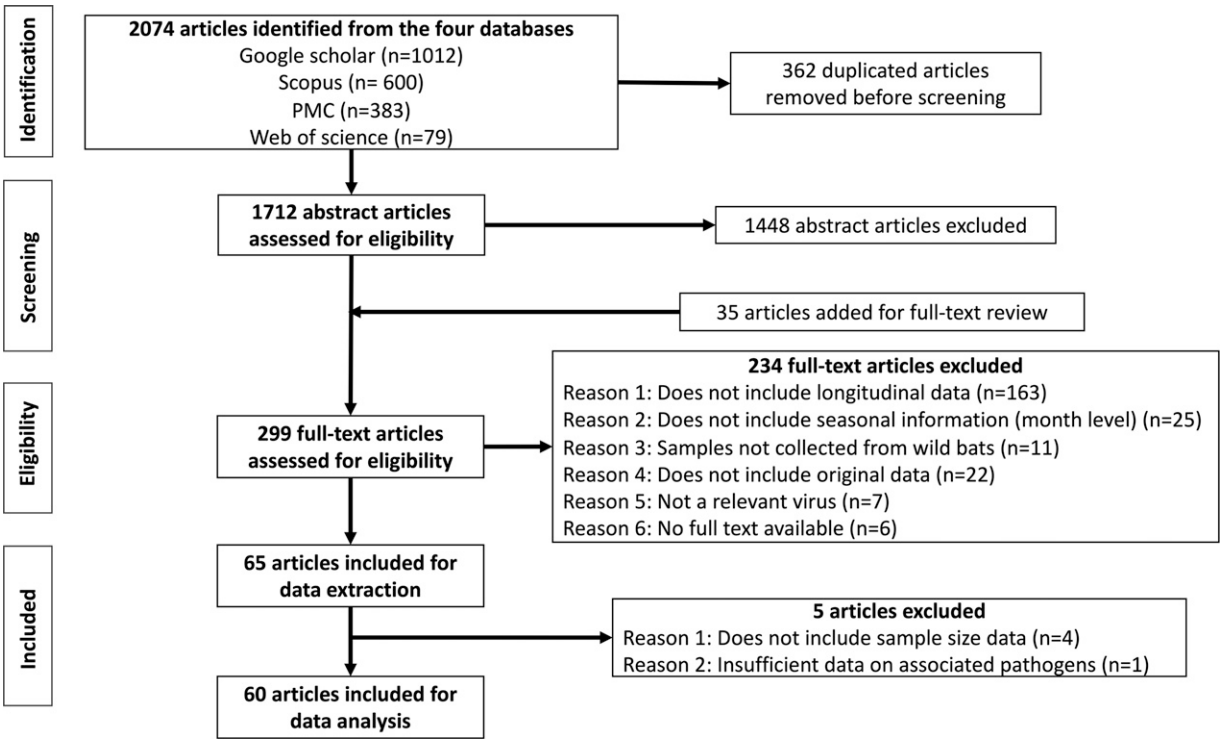

FIG. 1. PRISMA flow diagram. PRISMA flow diagram for the review aimed at investigating seasonal viral shedding patterns in bats. This review focuses on longitudinal studies about bat virus shedding and serology, with 60 included studies for data analysis spanning from 2001 to 2023.

distribution consistently fluctuated at similar levels across years. These data, along with consistent absolute and average peaks that occurred in March, showed a clear seasonal pattern, aligning with the weaning period when neonates matured into juveniles (Supplementary Fig. S3) (Joffrin et al., 2021; Hoarau et al., 2023).

Mormopterus francoismoutoui in Réunion and *Pteropus lylei* in Cambodia and Thailand also presented clear seasonal patterns of coronavirus shedding based on direct detections. Coronaviruses from *Mormopterus francoismoutoui* had consistent evident peaks in February and March and small peaks in December, with μ_E of 1.27 and CV_E of 0.27 (Fig. 2A). *Pteropus lylei* in Asia yielded μ_E 1.87 and CV_E 0.55, showing consistent peaks in June (Supplementary Fig. S4A and B). These seasonal viral patterns synchronized with species' life cycles. Their shedding peaks coincided with weaning seasons, reporting juvenile bats as a critical risk factor (Wacharapluesadee et al., 2018; Cappelle et al., 2021; Joffrin et al., 2022; Hoarau et al., 2023). December peaks from *Mormopterus francoismoutoui* aligned with their parturition seasons, which could be attributed to adult bats' altered immunological states during pregnancy (Epstein et al., 2013).

TABLE 1. SUMMARY OF THE DATASET COLLECTED FROM INCLUDED PUBLICATIONS

Virus family/genus	*No. of events*[a]	*No. of longitudinal events*[b]		*No. of references*
		Viral	*Serological*	
Astroviridae	168	163	0	6
Coronaviridae	419	278	0	21
Filoviridae	85	14	51	8
Rhabdoviridae (*Lyssavirus*)	285	28	141	13
Paramyxoviridae[c]	354	163	0	8
Cedar and Cedar-related viruses	66	37	20	3
Hendra and Hendra-related viruses	130	57	40	8
Nipah and Nipah-related viruses	115	71	22	4
Total	1622	811	274	60

Summary of the virus families or genera, sampling events, and references from a review investigating seasonal viral shedding patterns in bats. This review focuses on longitudinal studies about bat virus shedding and serology, with 60 included studies for data analysis spanning from 2001 to 2023.

[a]The total number of sampling events reported in the included publications.

[b]The number of longitudinal events, each with at least 10 bat samples and a minimum of three events per location.

[c]Any other paramyxoviruses not including Nipah, Hendra, and Cedar viruses.

Table 2. Entropy Values and Seasonal Patterns in Species-Level Analysis

Virus	*Continent*	*Species*	*E*[a]	μ_E[b]	CV_E[c]	*Absolute peak*[d]	*Average peak*[e]	*Seasonal pattern*	*Figures*
Astrovirus	Africa	*Mormopterus francoismoutoui*	1.40, 1.52, 0.70, 1.07, 1.22	1.18	0.27	March	March	Clear	Supplementary Figure S3
Coronavirus	Africa	*Mormopterus francoismoutoui*	0.88, 1.23, 1.24, 1.83, 1.19	1.27	0.27	February	February	Clear	Figure 2A and
	Asia	*Pteropus lylei*	1.93, 2.87, 0.81	1.87	0.55	June	June	Clear	Supplementary Figure S4
	Asia	*Rhinolophus sinicus*	0.29, 0.44, 0, 0.01 (Rectal and feces) /0.00, 0.81, 0.31, 0.93 (Respiratory)	0.18/ 0.51	1.18/ 0.85	April/ September	April/ September	Unclear	
Filovirus	Africa	*Rousettus aegyptiacus*	0.03, 0.08, 0, 0.18, 0.14	0.09	0.88	November-December	October	Clear	Supplementary Figure S5
Lyssavirus	Europe	*Myotis daubentonii*	0.69, 0.21, 0.24, 0.07, 0.03, 0.03, 0.22, 0.18	0.21	1.01	July	June	Clear	Figure 2C and
	Europe	*Myotis myotis*	1.00, 0.57, 0.24, 0.47, 0.69, 0.10, 0.00	0.44	0.80	September	September	Clear	Supplementary Figure S6
	Africa	*Eidolon helvum*	0.00, 0.01, 0.05, 0.05, 0.00	0.02	1.01	July	July	Unclear	
	Africa	*Eidolon helvum*	0.00, 0.13, 0.04	0.06	1.17	March	February	Unclear	
Paramyxovirus[f]	Africa	*Mormopterus francoismoutoui*	0.08, 0.98, 0.46, 0.61, 0.44 (Feces)/0.02, 0.14 (Urine)	0.51/ 0.08	0.64/ 1.02	July/ December	November/December	Unclear	Figure 2B and
									Supplementary Figure S7
	Africa	*Rousettus aegyptiacus*	0.79, 1.07, 2.18	1.35	0.54	July	July	Clear	
Cedar	Australia	*Pteropus alecto and Pteropus poliocephalus*	2.32, 1.74, 0.00	1.35	0.89	August	October	Unclear	Figure 2D and
									Supplementary Figure S8
	Australia	*Pteropus poliocephalus*	0.00, 3.58	1.79	1.41	November	November	Unclear	
Hendra	Australia	*Pteropus alecto and Pteropus poliocephalus*	0.67, 2.32, 1.00, 0.38	1.09	0.78	September	September	Unclear	Supplementary Figure S9
Nipah	Asia	*Pteropus lylei*	2.00, 1.05, 1.61	1.56	0.31	May	May	Clear	Supplementary Figure S10
	Asia	*Pteropus medius*	0.00, 0.48, 1.58, 2.00	1.02	0.92	June	June	Unclear	
Nipah-related[g]	Africa	*Eidolon dupreanum*	0.00, 0.61, 0.01, 0.04	0.16	1.82	February	February	Unclear	Supplementary Figure S11

Summary of the entropy values and seasonal patterns for 17 bat species and virus combinations, derived from our review of longitudinal studies on bat virus shedding and serology. The review includes data from 60 papers published between 2001 and 2023. Entropy measures the concentration of virus shedding or seropositivity at a given time of the year. Combinations with $\mu_E \geq median(E)$, $CV_E \leq mean(CV_E)$, and the absolute and average peaks distributed within the same or adjacent months are considered to have clear seasonal patterns.

[a]E presents yearly entropy values of monthly prevalence or seroprevalence across different years in each example. Some years only have one sampled month or all negative samples and yield entropy value as NA, which are not included in the table.

[b]μ_E represents the mean of yearly entropy values for each example, showing the average fluctuation of monthly prevalence or seroprevalence.

[c]CV_E represents the coefficient of variation of yearly entropy values, showing the consistency of the distribution across different years.

[d]Absolute peaks represents months with the highest prevalence peaks in the yearly distribution of each example.

[e]Average peaks represents months with the highest prevalence peaks in the average distribution of each example.

[f]Any other paramyxoviruses not including Nipah, Hendra, and Cedar viruses.

[g]Nipah-related viruses represent viruses identified by antigens from the Nipah virus through serological assays and were defined as henipavirus.

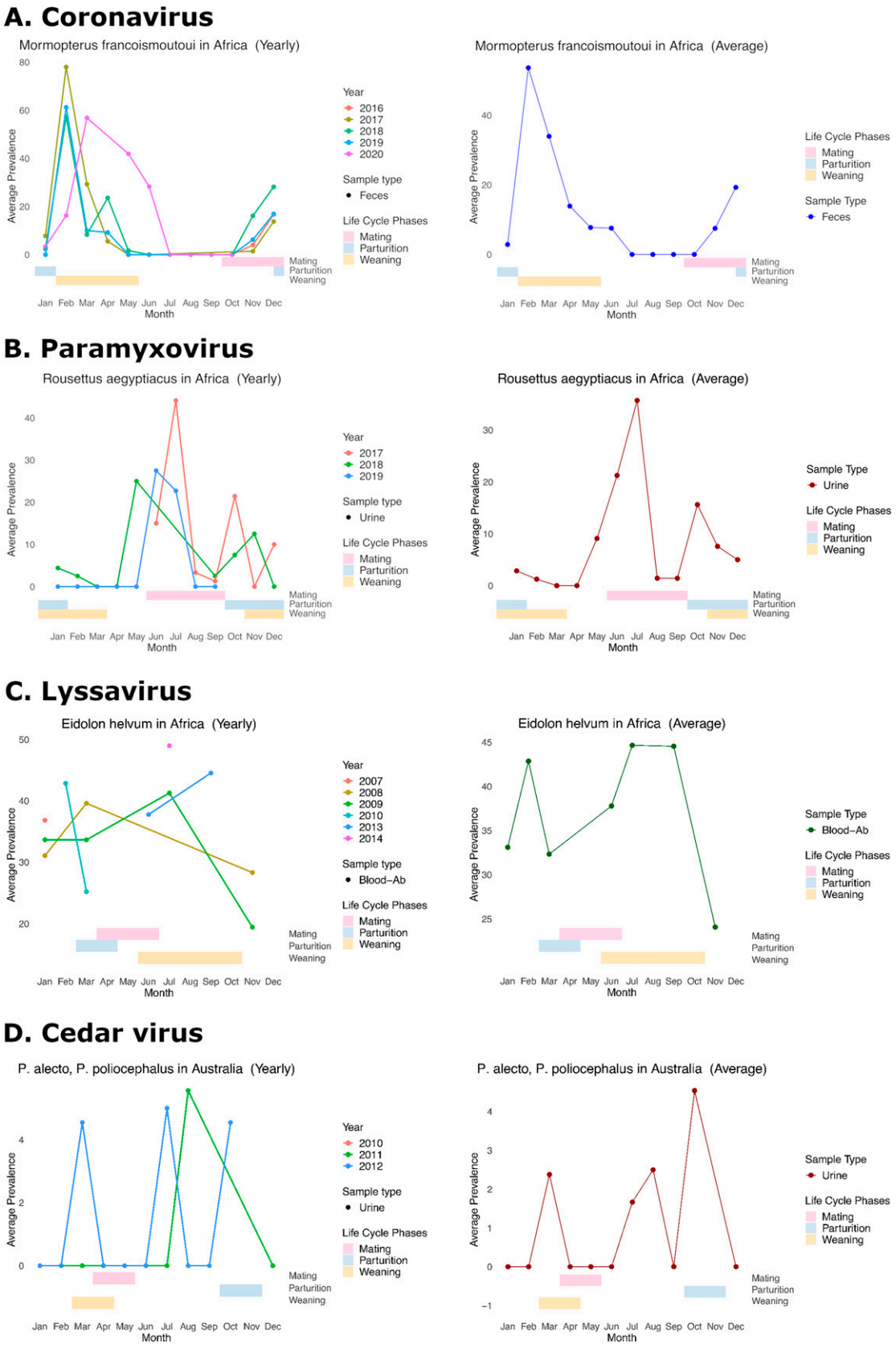

FIG. 2. Viral prevalence or seroprevalence in bat populations. Panels depict the prevalence or seroprevalence of four example bat-virus combinations out of our 17 species-level combinations we reviewed: two examples with clear seasonal patterns **(A** and **B)**, two examples without seasonality **(C** and **D)**. Each figure illustrates the yearly distribution (left) against the average distribution (right). **Rousettus aegyptiacus* has an asynchronous birthing season, which might sustain the circulation of viruses and make it challenging to assess the seasonality.

Serological evidence of filoviruses in *Rousettus aegyptiacus* from South Africa and Zambia presented a clear seasonal pattern based on their μ_E of 0.09 (exceeding 0.08), CV_E of 0.88 (less than 1.01), and consistent absolute and average peaks in adjacent months. The seroprevalence of filoviruses ascended to a peak from October to January and then decreased from February to April (Supplementary Fig. S5). Birthing pulses of *Rousettus aegyptiacus*, peaking from October to January, could increase their seroprevalence with maternal antibodies, while weaning seasons decreased the seroprevalence (Changula et al., 2018; Pawcska et al., 2018). However, the asynchronized birthing season in *Rousettus aegyptiacus* might also sustain the circulation of viruses in the population and make it challenging to assess the seasonality (Pawcska et al., 2018).

Lyssaviruses from *Myotis daubentonii* in the United Kingdom and *Myotis myotis* in Italy had clear seasonal patterns in seroprevalence. *Myotis daubentonii* presented consistent fluctuations across years with μ_E of 0.21, CV_E of 1.01, and peaks in seroprevalence in June or July, during or after parturition seasons in June (Supplementary Fig. S6A and B) (DL Horton et al., 2020). Similarly, the high μ_E and low CV_E from lyssaviruses in *Myotis myotis* along with their identical peaks in September provided evidence for a clear seasonal pattern (Supplementary Fig. S6C and D). However, unlike *Myotis daubentonii*, seroprevalence of lyssaviruses in *Myotis myotis* showed limited increases during parturition periods and decreased rapidly thereafter. They exhibited distinct seroprevalence pulses in September, placing additional emphasis on the seroprevalence peaks as a proxy for infection peaks after weaning periods (Kim et al., 2023). Moreover, both species reported extremely low seroprevalence following hibernation periods in spring.

There were two examples showing clear seasonal patterns in the *Paramyxoviridae* family. Paramyxoviruses from *Rousettus aegyptiacus* in South Africa had a clear seasonal pattern. The μ_E of 1.35 and CV_E of 0.54 showed consistently high seasonal peaks in direct viral detections, with absolute and average peaks occurring in July (Fig. 2D). Paramyxoviruses had prevalence peaks coinciding with the cold temperatures and limited food availability in winter without showing direct synchronicity with weaning or parturition seasons (Mortlock et al., 2019, 2021). Nipah viruses in *Pteropus lylei* from Thailand provided evidence for their clear seasonal patterns with μ_E of 1.56, CV_E of 0.31, and peaks in prevalence in May (Supplementary Fig. S10A and B). During May, *Pteropus lylei* in Thailand undergoes weaning, and juveniles began to depart from maternal dependence (Wacharapluesadee et al., 2010).

Examples without seasonality. The other 9 out of 17 examples did not show clear seasonal patterns. Some examples, like coronaviruses from *Rhinolophus sinicus*, lyssaviruses from *Eidolon helvum*, and paramyxoviruses from *Mormopterus francoismoutoui* had relatively low μ_E values, indicating their relatively uniform distribution across different seasons (Fig. 2C and Supplementary Fig. S4C and D). Some examples did not have continuously high variance, which is suggested by their high CV_E, such as Cedar and Hendra viruses from *Pteropus spp.* and Nipah-related viruses from *Eidolon dupreanum* (Supplementary Figs. S8, Figs. S9, Figs. and Figs. S11). Occasional peaks and high entropy values in some years could suggest that yearly factors, instead of seasonal factors, are more likely to impact the shedding pattern. For example, studies reported food deficiency for flying foxes in 2011, which might be the reason for the high prevalence of Cedar virus in 2011 (Field et al., 2011; Peel et al., 2019). Besides, asynchronous average and absolute peaks that occurred in Cedar viruses from *Pteropus spp.* also suggested their unclear seasonality (Fig. 2D).

Discussion

Our review has provided a comprehensive overview of longitudinal studies on bat viruses, highlighting evidence for the seasonal patterns of various viruses within bat populations. Our species-level analysis involved 11 bat species, focusing on particular host species to provide insights into viral shedding patterns directly from the viruses' reservoirs. The analysis revealed eight out of 17 bat-virus combinations showing clear seasonal patterns. Seasonal viral shedding or seroprevalence peaks often coincide with bats' life cycles, especially their weaning, parturition, or hibernation seasons. Other nine examples did not present clear seasonality because of their uniform distributions or random fluctuations.

Longitudinal data on bat viruses reflect a different landscape from viral studies in bat populations more generally. The observed prevalence of coronaviruses in bats corresponds with findings from other studies, while other viruses have a higher prevalence compared to surveillance studies (Harris et al., 2006; Rahman et al., 2013; Shivaprakash et al., 2021). This discrepancy may suggest that longitudinal studies were often conducted in regions that previously detected viruses. Furthermore, the sampling methods also have a significant impact on the reported prevalence and seroprevalence, showing a higher positive ratio in serological testing. Even within the same sampling category, different sampling methods could lead to asynchronous distributions. For instance, urine samples have shown a higher prevalence within the same species than feces samples for paramyxoviruses and resulted in peaks during different seasons. Besides, the geographical distribution of these viruses in our review is more concentrated compared to the broader scope of bat virus detection studies for some viruses (Olival and Hayman, 2014; XL Yang et al., 2017). This observation is reasonable, considering that longitudinal studies are often influenced by targeted research focus and the intensity of research efforts in specific regions. Importantly, most species in the species-level analysis are locally predominant, so the trends in these species may not reflect patterns of viral shedding across all bat species in an area, especially less abundant species. For instance, *Mormopterus francoismoutoui* is the most abundant bat species on Réunion Island, and Pteropus lylei is an endemic species in South Asia with a large population (Aguillon et al., 2023). Their localized abundance may facilitate the collection of longitudinal data from these bats within a restricted area.

Three primary factors may contribute to these observed seasonal patterns. First, juvenile bats play a critical role in virus prevalence peaks coinciding with or after the weaning period (Hurme et al., 2022; Muzeniek et al., 2022). This factor may explain peaks observed in *Mormopterus francoismoutoui* in Africa with coronaviruses and astroviruses, *Pteropus lylei* in Asia with coronaviruses and Nipah virus, and *Myotis myotis* in Europe with lyssaviruses. Juveniles experience waning of

maternal antibodies, along with increased physiological and nutritional stress due to separation from their mothers and the challenges of independent foraging (Epstein et al., 2013; Orłowska et al., 2020). These challenges may make them more prone to infections and result in higher viral shedding rates (Montecino-Latorre et al., 2020; Eby et al., 2023). Second, parturition seasons usually show shedding or seroprevalence peaks as well (Turmelle et al., 2010a). Newborns with maternal antibodies elevate seroprevalence, which explain lyssavirus seroprevalence pulses from *Myotis daubentonii* in Europe (Peel et al., 2018). Besides, the temporary immunosuppression during pregnancy may render female bats more susceptible to infections (French et al., 2009; Breed et al., 2011; Changula et al., 2018). This factor might explain the less pronounced peaks in November or December from *Mormopterus francoismoutoui* in Africa with coronavirus and astrovirus. Third, hibernation may contribute to fluctuations in seroprevalence. During hibernation, bats exhibit a reduction in physical activities, metabolic rate, and immune response, which may cause the low lyssavirus seroprevalence observed in early spring across European bat populations (Meteyer et al., 2012; Lilley et al., 2017). After exiting hibernation, the seroprevalence pulses observed later could be explained by maternal antibodies from newborns, as seen in peaks in *Myotis daubentonii*, or by increased infection rates after hibernation and weaning seasons, as seen in peaks in *Myotis myotis* (DL Horton et al., 2020; Kim et al., 2023).

In addition to the importance of reproductive periods on the seasonality of viral infections in bats, there are other factors like anthropogenic activities that can influence these patterns. In our 60 included papers, none focus specifically on the impact of human activities on viral shedding. However, outside of these papers, there is evidence for this point. For example, some studies demonstrated that changes in human land use can alter bat ecology, causing nutritional stress in bats, which then increases Hendra virus shedding within bat populations (Becker et al., 2023). This increased shedding, combined with more frequent contact between bats and domestic horses, results in a higher risk of Hendra virus spillover. Additionally, stress from arousal out of hibernation might reactivate herpesviruses from latency, causing viremia (Gerow et al., 2019). Beyond these direct findings, some studies indicated that stress affects immune responses in bats, potentially increasing viral loads, while others noted that human activities often impact animal habitats and lead to nutritional stress (Becker et al., 2015; Subudhi et al., 2019). Given these findings, human activities, such as habitat disruption and interference with hibernation, may contribute to increased viral shedding in bats due to stress. However, this research should ideally be done in the context of longitudinal studies that can account for the effects of anthropogenic stressors on top of natural cycles of virus transmission.

Our review still has several limitations. First, longitudinal data on bat viruses are very limited. Most studies reported less than five years of data, making it difficult to determine consistent seasonality. However, our research did identify evidence for seasonal patterns in some bat species for some viruses, like coronaviruses in *Mormopterus francoismoutoui* and paramyxoviruses in *Rousettus aegyptiacus*. Furthermore, some viruses, like lyssaviruses and filoviruses, primarily used serological testing, which is not a direct indicator of current viral shedding. Although studies have reported that shedding levels for certain viruses may correlate with antibody titers in bat populations, using serology as an alternative measure for viral shedding is not always accurate across all viruses (Peel et al., 2018). For instance, bats might have low susceptibility and low antibody titers for rabies at the same time, making it challenging to infer viral shedding due to infections from serological data (Turmelle et al., 2010b). Therefore, even though longitudinal serological data may reflect trends in antibody dynamics and indicate potential viral shedding patterns, interpreting viral shedding patterns from serological data should be performed with caution, especially if there is limited data on viral shedding that can be used to validate seasonal patterns in serological time series. Lastly, the direct correlation between viral shedding and zoonotic spillover events remains unclear. Some viruses have shedding pulses coinciding with spillover peaks, like Hendra viruses and Marburg viruses, while other viruses do not show an obvious alignment, such as Nipah viruses (Amman et al., 2012; Peel et al., 2019; Epstein et al., 2020). This misalignment may occur because we missed shedding pulses happening in outbreak areas. For instance, Nipah viruses show different seasonal patterns between strains, locations, and bat populations (Epstein et al., 2020). If spillovers happened in areas or bat populations different from those monitored in longitudinal studies, the shedding pulses related to spillovers would be missed. Our findings on seasonal shedding patterns could provide targeted periods to prevent spillovers for viruses with aligned peaks but may have limited effect for those without aligned peaks.

Based on our findings and limitations, we propose several recommendations for future studies. Longitudinal studies with a combination of direct viral testing and serological testing on young bats could significantly advance our understanding of immunity dynamics and viral shedding in bat populations. Our review highlights the pivotal role of reproductive cycles, particularly emphasizing juveniles and weaning periods because of maternal antibody waning (Peel et al., 2018). Thus, methodically targeting newborns or pups from the parturition seasons to the subsequent growth stages is essential to track maternal antibody dynamics. However, continuously tracking the same bats is always resource-intensive, and it might be more feasible to explore this question from a population perspective. Recording demographic characteristics like weight, age, sex, and reproductive status would provide a more thorough understanding of bat populations' status (Krochmal and Sparks, 2007; Peel et al., 2018). Combining serological and viral testing, dynamic models, and detailed demographic data, such studies could deepen our knowledge of how maternal antibodies and pathogen transmission interact during bat's life cycles at a population level, providing valuable perspectives on disease transmission and immunity in these key wildlife reservoirs. Furthermore, extending longitudinal studies to other regions would be beneficial to gain a more comprehensive understanding of seasonal viral shedding in bats. The disparity between the known distribution of bat viruses and that of longitudinal research provides numerous regions as prime candidates for extended study. For example, antibodies against filoviruses were detected in Asia and both coronaviruses and paramyxoviruses were detected in Brazil, while none were reported with longitudinal data in our review (Olival and Hayman, 2014; Weber and da Silva, 2023).

Delving into the distinctive climatic conditions and varied ecosystems could reveal critical risk factors of viral shedding (Eby et al., 2023). Simultaneously, consistent sample types for each virus, like feces for coronaviruses and urine for paramyxoviruses, could ensure comparability of our results (Baker et al., 2012; Cohen et al., 2023).

In conclusion, this study has pinpointed representative seasons with viral shedding pulses and several critical factors that affect the seasonal patterns of viral shedding in bats, providing valuable information for strategies to prevent zoonotic spillover events. According to our analysis, some bat-virus combinations exhibit elevated viral shedding during parturition and weaning seasons or increased susceptibility during posthibernation phases. Integrating these risk factors with observed seasonal patterns allows for a more precise prediction of high-risk periods for viral shedding from bats. Our findings provide support for interventions targeting these pivotal periods, especially for those pathogens with aligned shedding pulses and spillover risks (Amman et al., 2012; Peel et al., 2019). Interventions such as issuing alerts from the local government to inform residents about heightened prevalence, paired with efforts to protect bats by closing caves or fencing off roost areas, would enable them to avoid contact with bats (Runge et al., 2020). When contact with bats is unavoidable for some communities (*e.g.,* hunters, bat biologists, wildlife rehabilitators), usage of personal protective equipment (PPE) is highly recommended (Garland-Lewis et al., 2017), regardless of time of year or viral prevalence. Government initiatives to encourage and provide necessary personal protective equipment could be a practical public health strategy that could be targeted to higher-risk time periods. These measures are instrumental in reducing human–bat direct interactions during shedding pulses, thereby decreasing the risk of viral transmission from bats to humans and enhancing public health.

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Supplementary Material

Supplementary Figure S1
Supplementary Figure S2
Supplementary Figure S3
Supplementary Figure S4
Supplementary Figure S5
Supplementary Figure S6
Supplementary Figure S7
Supplementary Figure S8
Supplementary Figure S9
Supplementary Figure S10
Supplementary Figure S11
Supplementary Table S1
Supplementary Table S2
Supplementary Table S3
Supplementary Table S4
Supplementary Data

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