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Two (or more) viruses in one bat: a systematic quantitative literature review of viral coinfection in bats

Eli J. Kaufman
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Two (or more) viruses in one bat: a systematic quantitative literature review of
viral coinfection in bats

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Completed Remotely

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Major: Biology

Submitted in partial fulfillment of the requirements for Australia: Rainforest, Reef, and Cultural
Ecology, SIT Study Abroad, Spring 2020

Abstract:

Viral coinfection is an important topic in pathogen dynamics, and can increase viral shedding and change disease outcomes. As bats are carriers of important zoonoses, such as the SARS coronaviruses, rabies, and other deadly viruses, knowing more about their coinfection dynamics is important. This quantitative systematic literature review sought to show how many papers reported bat viral coinfections, and created three databases. The first database, the SQLR database was based on searches for coinfections. The second database, the Astrovirus database was to determine how much of the literature was being missed by examining a single viral family more in depth and determining how many papers were identified in the SQLR database. The third database focused on *Dependoparvovirus*, a viral genus which has been thought to require coinfection in the past. A total of 725 coinfecting bats became a part of the SQLR database. The studies were mostly done in Asia, and a few trends in bat and viral families appeared. Bat field virology has a lot of valuable data, and not all of it is reported in an accessible way.

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Acknowledgements:

Thank you to Dr. Alison Peel, who introduced me to the world of bat coinfection, and who guided and mentored me through the Systematic Quantitative Literature Review process. Thank you to SIT and their staff, Tony Cummings, Jack Grant, and Vanessa Messmer, for teaching and supporting me throughout this semester.

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Introduction:

Bats host more zoonotic viruses per species than other mammalian orders, and are an important wildlife consideration when it comes to threats to human wellbeing (Luis et al. 2013). Bats are thought to be the source of considerable viral diversity due to their ability to fly, and their colonial social behavior (O’Shea et al. 2014, Calisher et al. 2006). It is important to learn more about bats and their dynamics as hosts, not only to understand viruses and their spillover potential, but for bats and their own ecological and economic value (Kasso and Balakrishnan 2013). Coinfection in bats is common, and has significant impacts on viral shedding, symptoms, and severity of disease (Anthony et al. 2013, Peel et al. 2019, Christina et al. 2018). While coinfection between viral, bacterial, fungal, and parasitic pathogens all occur in bats, this paper focuses on the literature available on viral coinfections.

Viral coinfections can be between two or more viruses in the same family (intrafamilial), or between two or more viruses in different families (interfamilial). Coinfections reported in literature are often reported incidentally, or as a byproduct of molecular investigations not specifically seeking coinfection. As such, papers may be missed by searches specifically for coinfection. Astroviruses are a family of viruses, selected for a more thorough investigation of coinfection in order estimate how many papers were missed for other families of viruses.

Dependoparvovirus is a genus of parvoviruses, also known as Adenovirus Associated Viruses (AAVs), or Dependoviruses, and some of the members are thought to require coinfection with a DNA virus, or a ‘helper virus’ for efficient replication. *Dependoparvoviruses* were first discovered replicating with adenovirus, but since with other viruses, including herpesviruses (Atchison et al. 1965, Buller et al. 1981). Other species, placed in the genus because of genetic similarity are autonomous, replicating seemingly without coinfection of a helper virus (Brown et

al. 2005). As *Dependoparvoviruses* are usually found coinfecting with other viruses, there were searches targeting them, and a separate database was created for them.

Two scientific search engines were selected for their database size and peer reviewed nature, and searches were run to investigate the literature reporting coinfections in bats and its accessibility. Databases were created in order to investigate the literature, how the literature reported coinfections, where there are commonalities in the literature, and where there are gaps.

Methods:

Searches

Searches were conducted on Scopus and Web of Science in late April 2020. A total of 10 searches were conducted, the first six of which with keywords bat, virus, and variations on the theme of coinfection. The seventh and eighth were general searches targeting bat astroviruses, and the ninth and tenth searches were general searches targeting *Dependoparvoviruses*. The Scopus searches were run from the advanced search, looking through the Scopus databases' Document Titles, Abstracts, and Document Keywords either generated by Scopus or by the paper author. The Web of Science searches were run from the advanced search, looking through the Web of Science Core Collection with the Topic Field, which searches Title, Abstract, Author Keywords, and Web of Science's 'Keywords Plus®.'

Table 1: Searches

Search #	Database	Query
Search 1	Scopus	TITLE-ABS-KEY (bat AND virus AND coinfection OR co-infection OR coexistence OR co-existence OR cocirculation OR co-circulation OR synchronous)
Search 2	Web of Science	TS=((bat AND virus) AND (coinfection OR co-infection OR coexistence OR co-existence OR cocirculation OR co-circulation OR synchronous))
Search 3	Scopus	TITLE-ABS-KEY (bat AND virus AND family AND primer)
Search 4	Web of Science	TS=(bat AND virus AND family AND primer)
Search 5	Scopus	TITLE-ABS-KEY (bat AND virus AND coinfect* OR co-infect* OR coexist* OR co-exist* OR cocirculat* OR co-circulat* OR synchronous)
Search 6	Web of Science	TS=((bat AND virus) AND (coinfect* OR co-infect* OR coexist* OR co-exist* OR cocirculat* OR co-circulat* OR synchronous))
Search 7	Scopus	TITLE-ABS-KEY (bat AND virus AND astro*)
Search 8	Web of Science	TS=(bat AND virus AND astro*)
Search 9	Scopus	TITLE-ABS-KEY (bat AND virus AND dependoparvovirus OR aav OR dependovirus OR adeno-associated)
Search 10	Web of Science	TS=((bat AND virus) AND (dependoparvovirus OR aav OR dependovirus OR adeno-associated))

Titles were read and if deemed relevant, abstracts, and then the body of the paper. Relevance was determined by fitting inclusion criteria, as follows. Papers were credited to the first search that located them.

Three databases were created. The SQLR database was created in order to investigate the body of literature available on scientific search engines with viral coinfections in bats. The Astrovirus database was created in order to estimate how much literature was being missed by the SQLR database, by using more general search terms on bat viruses in a specific family. The *Dependoparvovirus* database was created to investigate a particular viral genus's infection in bats, which is thought to largely rely on coinfection for successful replication.

In order to be included in the SQLR database, papers must

- Have originated from the first 6 searches, or from the references of papers which fit the inclusion criteria from the first 6 searches
- Present original research and report infection of bats with viruses
- Samples must not be pooled between individual bats, or be pooled and tested in such a way that combinations of viruses in individual bats is still reported.
- Detection of viral infection must be by molecular means, either PCR or some form of metagenomic analysis.
- Multiple viruses must be reported from individual bats, and it must be possible to determine to the family level what viruses were present.
- The study must declare that two viruses detected are separate strains, genotypes, or species. Studies that merely report nucleotide % identity differences are not eligible for inclusion.

- The data must be provided in written text in the body of the paper, in tables either published with the papers, or in supplemental files published with the paper. Papers that provided data in phylogenetic trees that did not mention co-infection in the legend was not included.
- Papers reporting coinfections in individuals by identifying new viruses in previously tested samples were included.

In order to be included in the astrovirus database, papers must

- Fit the inclusion criteria from the SQLR database, but instead originate from the seventh or eighth search, or the references of papers from the seventh and eighth searches.

In order to be included in the *Dependoparvovirus* database, papers must

- Fit the inclusion criteria from the SQLR database, but originate from any search, or any of the references of papers which fit inclusion criteria from any database. Additionally, papers which do not report coinfection in individuals, and papers that have pooled samples, but do report *Dependoparvoviruses* in bats are also included.

Papers deemed to have fit the inclusion criteria of a paper within a database's references were dealt with in the same way as if they were found from that search instead.

See Appendix 1 for the literature in the SQLR, Astrovirus, and *Dependoparvovirus* databases.

Data Extraction

Papers that fit the inclusion criteria for any of the databases then had various pieces of information extracted from them. Title, Authors, Year Published, Journal, Continent, Country, State/Province/Department/Region, and the city of the first affiliation of the first author were

recorded. Whether or not the terms zoon*, or coinfect*/co-infect* were used in the body of the paper or in the figure legends was recorded. The method of sample collection, sample processing, whether or not the samples were pooled, whether or not PCR products were cloned to look for intrafamilial coinfections, and whether or not the paper relied on a previous paper's results to report coinfections. Oral, throat, pharyngeal and nasopharyngeal samples were all classified as oral. The family, genus and species of the bats in which coinfection was detected were all recorded. The families of viruses that could have been detected in the paper were recorded, as were the families of viruses that were recorded as coinfecting within bat individuals. The identity of the viruses coinfecting individual bats was recorded in as much specificity as possible in order to retain the most information when doing analysis, but at least to the family level.

Data on what families were tested for, as well as whether or not PCR products were cloned came only from the body of the original paper. When papers referenced other papers in their references, or simply referred to methods in other papers only sometimes was that data tracked down.

Results:

Searches

There was a total of 115 unique search results in Web of Science Searches 2, 4, and 6 from which the SQLR database was formed. There were 53 new search results in Search 8 that were not found in Searches 2, 4, or 6, and all 18 search results from search 10 were not found on searches 2, 4, or 6.

8 papers were eligible for the Astrovirus database. There were 3 that were identified in the general searches 1-6, and 5 that were not, meaning that at least 62.5 % (5/8) of the literature on coinfections in astroviruses was not discovered by my general searches.

Table 2: Searches and composition of databases

Search #	Database	Results	SQLR	Dependoparvovirus	Astrovirus
Search 1	Scopus	57	9	0	1
Search 2	Web of Science	58	1	0	0
Search 3	Scopus	22	3	0	2
Search 4	Web of Science	23	3	1	0
Search 5	Scopus	84	1	0	0
Search 6	Web of Science	93	0	0	0
Search 7	Scopus	60	0	1	4
Search 8	Web of Science	60	0	1	1
Search 9	Scopus	19	0	3	0
Search 10	Web of Science	18	0	1	0
References	-	-	4	0	0
Sum	-	-	21	7	8

Databases

Of 8 papers that qualified for the astrovirus database, 5 had not been detected in the 6 coinfection-oriented searches, and 3 had. Of the 7 papers that qualified for the *Dependoparvovirus* database, 1 qualified for the SQLR database. There was no overlap between the astrovirus database and the *Dependoparvovirus* database.

Coinfections – SQLR Database

1059 viruses were reported in 527 intrafamilial coinfections. 1,046 of them were in reported coinfections with two viruses in an individual bat. 3 of the intrafamilial coinfections were of 3 different strains of the same families, one in the rubula paramyxovirus subfamily and

two in the betacoronaviruses. One intrafamilial coinfection was of four different filoviruses detected in an individual bat.

Intrafamilial coinfections were detected in 8 viral families. There were 18 adenoviruses, 18 astroviruses, 106 coronaviruses, 4 filoviruses, 882 herpesviruses, 27 paramyxoviruses, and 4 retroviruses in intrafamilial coinfections. There were no intrafamilial coinfections found in bornaviruses, circoviruses, parvoviruses, polyomaviruses, or rhabdoviruses, despite there being interfamilial coinfection detected in those families.

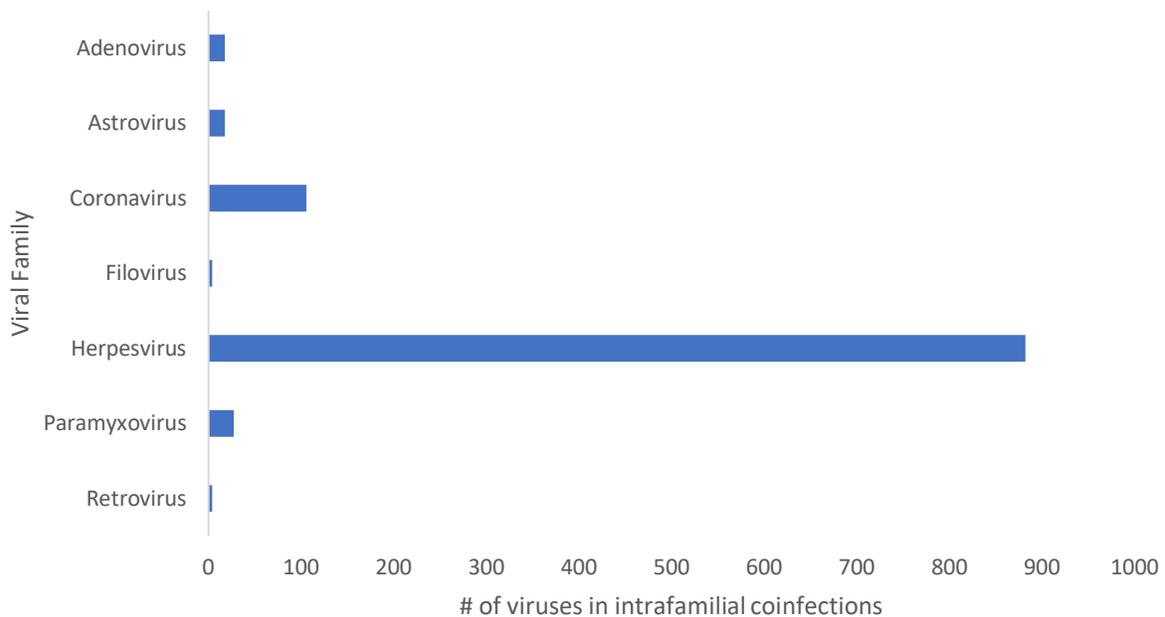


Figure 1: Number of viruses in intrafamilial coinfections in different families from the SQLR Database.

401 viruses were reported in 198 interfamilial coinfections. 194 of them were coinfections with two viruses in an individual bat. All four of the other coinfections had 3 families of viruses detected in a single bat, and one of those also had an additional intrafamilial coinfection of retroviruses.

Interfamilial coinfections were detected in 11 viral families. There were 111 adenoviruses, 14 astroviruses, 4 bornaviruses, 24 circoviruses, 52 coronaviruses, 119 herpesviruses, 42 paramyxoviruses, 4 parvoviruses, 5 retroviruses, 10 polyomaviruses, and 2 rhabdoviruses in interfamilial coinfections. There were no filoviruses in interfamilial coinfections, despite there being intrafamilial filovirus coinfection detected.

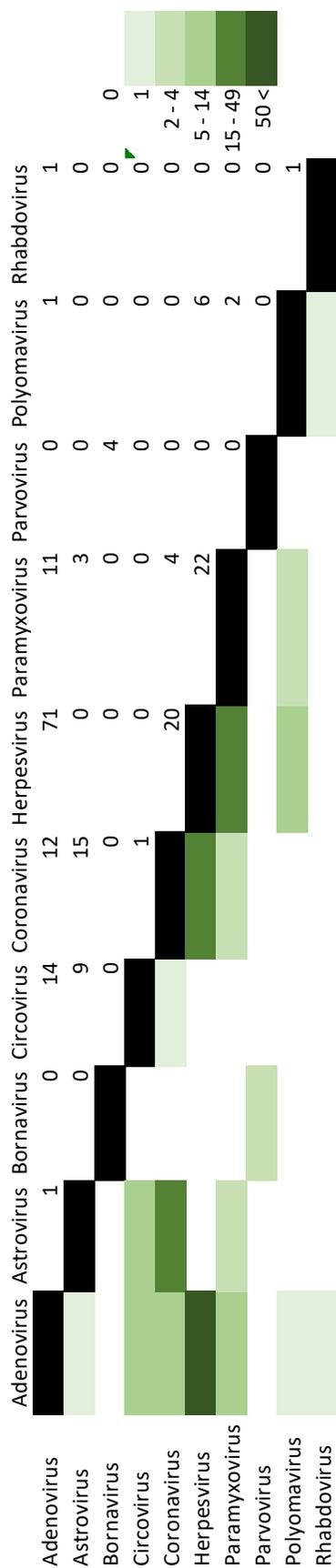


Figure 2: Interfamilial coinfection heatmap of coinfections of only 2 viruses. Color legend to the side, and the numbers are

in the top right half of the figure, while the heatmap is in the bottom left of the figure. Data is from SQLR Database.

The most common interfamilial coinfection detected with only two viruses was between adenovirus and herpesvirus with 71 individuals reported. Following that, herpesvirus and paramyxovirus with 22, coronavirus and herpesvirus with 20, astrovirus and coronavirus with 15, adenovirus and circovirus with 14, adenovirus and coronavirus with 12, adenovirus and paramyxovirus with 11, astrovirus and circovirus with 9, herpesvirus and polyomavirus with 6, coronavirus and paramyxovirus with 4, astrovirus and paramyxovirus with 3, and paramyxovirus and polyomavirus with 2. Adenovirus and astrovirus, adenovirus and polyomavirus, adenovirus and rhabdovirus, circovirus and coronavirus, and polyomavirus and rhabdovirus each had one coinfection. There were no coinfections between herpesvirus and either astrovirus or circovirus, paramyxovirus and circovirus, parvovirus and adenovirus, astrovirus, circovirus, coronavirus, herpesvirus, or paramyxovirus, polyomavirus and astrovirus, circovirus, coronavirus, or parvovirus, or

rhabdovirus and astrovirus, circovirus, coronavirus, herpesvirus, paramyxovirus or parvovirus.

There were also 4 interfamilial coinfections with more than 2 families of viruses. All of these interfamilial coinfections came from a single paper by Escalera-Zamudio et al. 2017, and consisted of three triple family coinfections. Three of the triple family coinfections were of a gammaretrovirus, a *Dependoparvovirus*, and a bornavirus in two *Desmodus rotundus* and a *Diphylla ecaudata*. The fourth was a *Diphylla ecaudata* coinfecting with a betaretrovirus, a gammaretrovirus, a *Dependoparvovirus*, and a bornavirus. This *Diphylla ecaudata* was the only individual reported as both interfamilial and intrafamilial coinfections.

16 out of 21 papers in the coinfection database had intrafamilial coinfections. 15 of the papers only detailed a single families intrafamilial coinfections, while Anthony et al. 2013 detailed three families intrafamilial coinfections. Intrafamilial coronavirus coinfections were reported in 7 papers, the highest number of papers reporting any one families intrafamilial coinfections. Intrafamilial coinfections of herpesvirus and paramyxoviruses were reported in 3 papers, astroviruses in 2 papers, and adenoviruses, filoviruses, and retroviruses each in 1 paper.

8 of 21 papers in the coinfection database had interfamilial coinfections. 2 of the papers with interfamilial coinfections only detailed coinfections between two families. 3 of the papers with interfamilial coinfections reported coinfections between three families, 2 of the papers with interfamilial coinfections reported coinfections between four families, and 1 paper, Anthony et al. 2013, reported interfamilial coinfections between 6 different viral families. Both adenovirus and coronavirus were reported as having interfamilial coinfections in five papers. Following that, interfamilial coinfection was reported in 4 papers with paramyxovirus, 3 papers with astrovirus, and 2 papers with herpesvirus and polyomavirus. Interfamilial coinfections in bornavirus, circovirus, parvovirus, and retrovirus were reported in only a single study each.

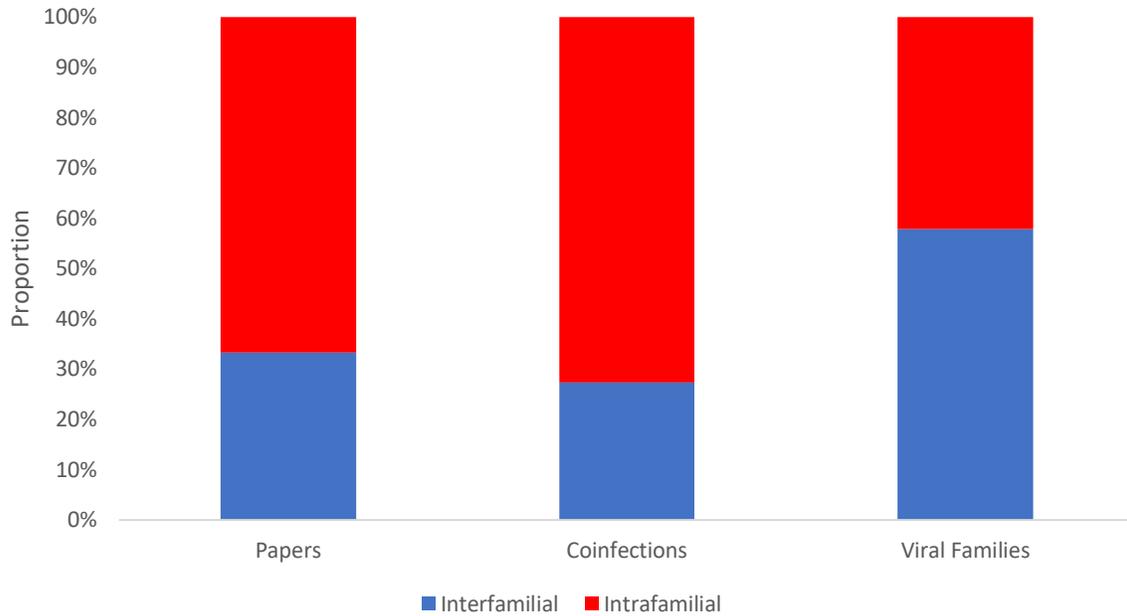


Figure 3: Papers reporting interfamilial and intrafamilial coinfections, number of interfamilial and intrafamilial coinfections and number of viral families found in interfamilial and intrafamilial coinfections.

Coinfections – *Dependoparvoviruses*

A total of 166 *Dependoparvoviruses* were detected in 4 studies that reported on non-pooled bat specimens. 55 *Dependoparvoviruses* were reported as coinfecting in 3 studies that reported non-pooled specimens. 9 *Dependoparvoviruses* were in intrafamilial coinfections with other *Dependoparvoviruses*. 46 were in interfamilial coinfections, 42 with an adenovirus, and 4 with multiple other families in the same individual. 1 study reported *Dependoparvovirus* infection in 4 different individuals, and coinfection of other parvoviruses, but not *Dependoparvovirus*. Another 3 studies each reported *Dependoparvovirus* sequences from pools of specimens from multiple bats.

Papers

SQLR: Papers were published in 15 journals, twice in Emerging Infectious Diseases and Journal of Virology, and three times in both Ecohealth and Virologica Sinica. Lau is the only first author who features multiple papers in the SQLR database, contributing three papers. The range of years in which papers were published and made it into the SQLR database was from 2007, to 2019. The median year was 2016, and the mean year 2014. The most papers published in a single year was six papers published in 2017.

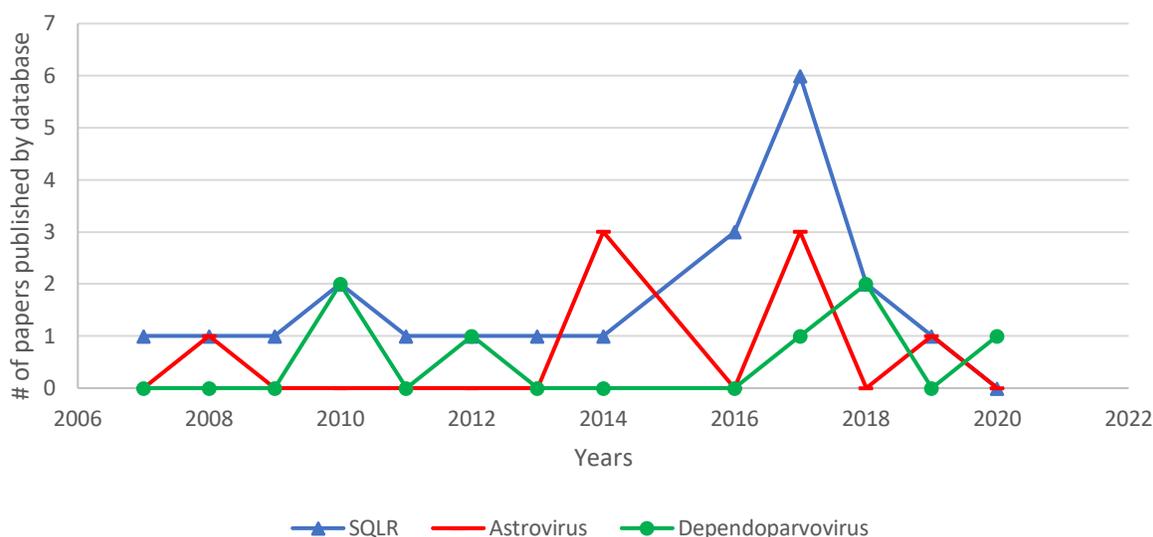


Figure 4: Number of papers published by database and year

Dependoparvovirus: Papers were published in 5 journals, twice in Journal of General Virology and in the Journal of Virology, once in Viruses, Ecohealth, and Scientific Reports. No first author published more than once. The range of years was 2010-2020. The median year was 2017, and the mean 2015. There were two papers published in 2010, and two papers published in 2018.

Astrovirus: Papers were published in 7 journals, with only PLoS ONE featuring twice. No individual researcher was first author on more than one paper. The range of years was 2008-2017. The median year was between 2014 and 2017. The mean year was 2015. There were 3

papers published in 2014, and 3 papers published in 2017, all other papers were the only papers in the database on their year.

Geography

SQLR: There were 2 papers published in N. America, 5 in Africa, and 12 in Asia, and 2 in Europe. 8 papers were from China, 2 from Kenya, and 1 each from Germany, Bangladesh, Guatemala, Malaysia, Italy, Mexico, Indonesia, and South Africa. Another paper was published by French researchers in the French Department of Reunion with samples from the Union of Comoros, Mauritius, and Madagascar. The city of the top affiliation of the first author was most commonly Hong Kong with 4 papers, followed by Berlin and Wuhan with 3 each, Atlanta and New York with 2 each, and Sainte-Clotilde, Beijing, Guangzhou, Jinan, Torino, Sapporo, and Pretoria with 1 each.

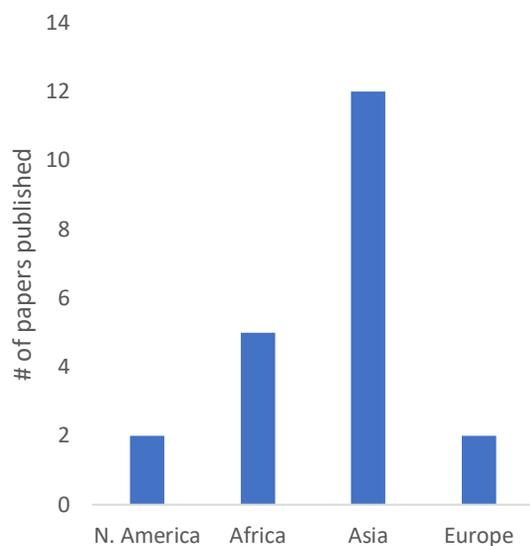


Figure 5: Number of papers published by continent in the SQLR database.

Continents not featured did not have any papers in the SQLR database.

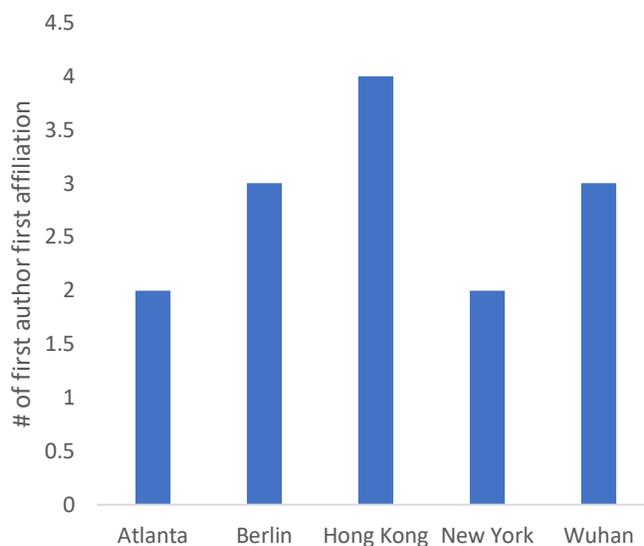


Figure 6: Number of first author affiliations by city for the cities that had more than 1 in the SQLR database

database

Dependoparvovirus: 2 papers published in N. America, 1 in S. America, and 4 in Asia. The 4 Asian papers were published in China, and the others were published in the USA, Brazil, and Mexico. 2 papers first author first affiliations were to Wuhan, China, and all other cities were not repeated.

Astrovirus: There was 1 paper published in Africa, 5 in Asia, and 2 in Europe. There were 3 papers published in China, and a single paper published in Hungary, France, Malaysia, Kenya and in Saudi Arabia each. There was no city which featured multiple times in first author first affiliations.

Sample Collection

SQLR: The most common form of sample collection was a swab, with 17 papers using some form of swab to collect a specimen from a bat. However, four papers used only blood or tissue. Fecal samples were the most common specimen collected, with 12 papers reporting the collection of feces. Following that was an oral swab in 10 papers, tissue in 8 papers, and an anal swab in 7 papers. Both urine and blood were used in 4 papers each.

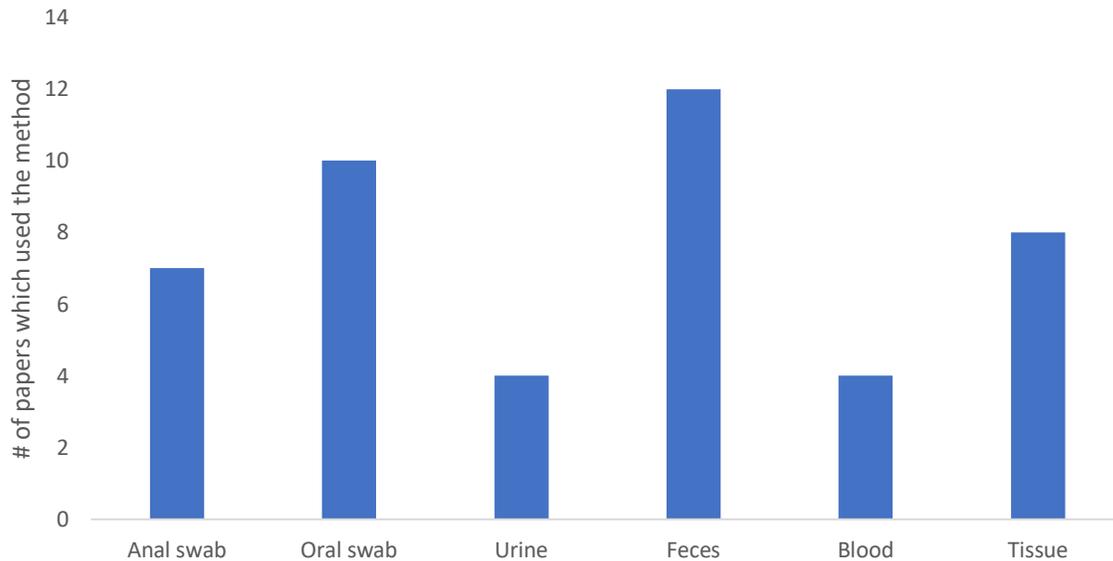


Figure 7: Number of papers which used collected this specimen type in the SQLR database.

Dependoparvovirus: Feces and tissue were used in 4 studies each, oral swabs were used in 2 studies, and anal swabs were used in a single study. Urine and blood were used in none.

Astrovirus: Fecal samples were the most commonly collected specimen from a bat, with 5 papers collecting feces. Following that, 3 papers collected anal swabs, 2 collected oral swabs or used tissue, and only a single study collected urine or blood.

Sample Processing

SQLR: PCR was used in every paper to detect molecular evidence of viruses. 11 of the papers relied on cloning their PCR products to detect viral coinfections, while 10 did not. Only 2 of the papers, Rizzo et al. 2017 and Escalera-Zumundio et al. 2018 used metagenomic techniques to investigate infections in bats. 3 papers relied on previous studies to determine if there were coinfections in their samples. Chu et al. 2008, Conrardy et al., and Wada et al. 2018 were each studies that processed samples which had already undergone molecular testing.

Dependoparvovirus: In 6 of the paper's PCR was used, and in only 2 of them were the PCR products cloned. Metagenomics were used in 4 of the papers. In 3 of the papers the samples were pooled between different bats, and in none of them were the coinfections reported reliant on previous papers data.

Astrovirus: All 8 papers used PCR to process samples, and 7 cloned their PCR products. 2 used metagenomics to analyze their samples. 1 paper, Chu et al. 2008 relied on 3 other papers to report coinfections: Chu et al. 2008, Chu et al. 2006, and Poon et al. 2005.

Verbiage

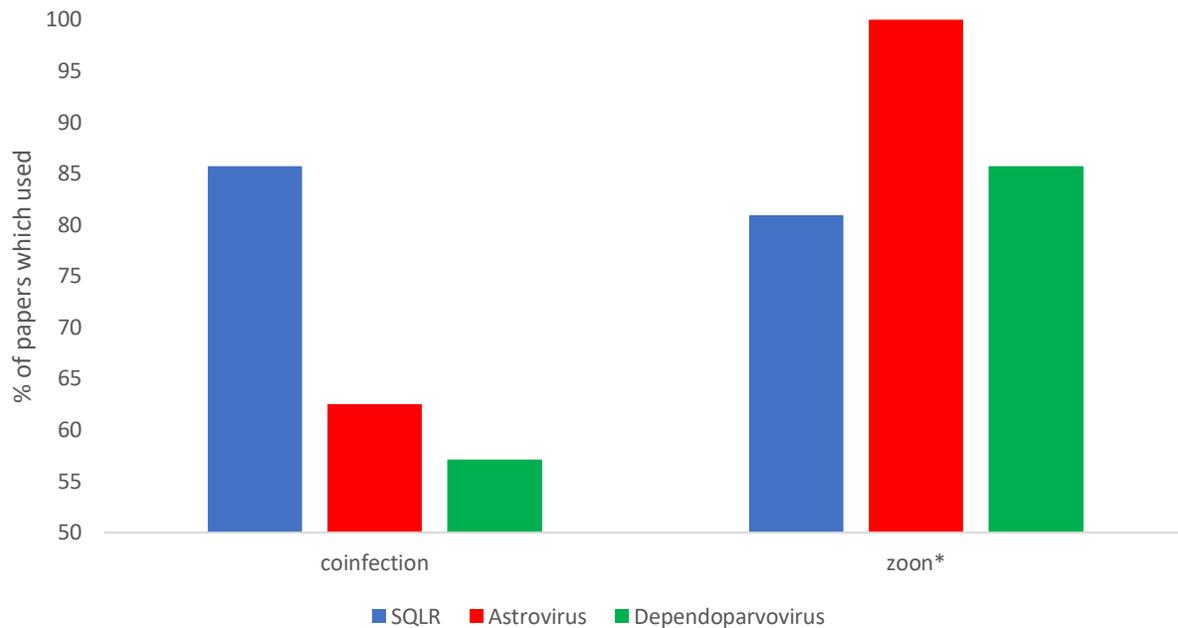


Figure 8: Percentage of the papers in each database which used the word in question. Coinfection was represented by coinfect* and co-infect* in the searches.

SQLR: 17 of 21 of the papers used some form of the word zoonosis. 18 of 21 of the papers used some form of the word coinfection.

Dependoparvovirus: 6 of 7 of the papers used zoon*, and 4 of 7 used coinfect*.

Astrovirus: All 8 of 8 papers used zoon*, and 5 of 8 used coinfect*.

Bats

Families

SQLR: All papers reported the family of the bats which had viral coinfections. 19 papers reported coinfections in only 1 family of bats. One paper, Ge et al. 2016 reported coinfections in 3 families, and another paper, Liang et al. 2017 reported coinfections in 2 families. A total of 7

families were reported in the 21 papers. 6 papers reported Miniopteridae, 6 papers reported Pteropodidae, 4 papers reported Vespertilionidae, 3 papers reported Rhinolophidae, 2 papers reported Hipposideridae and Phyllostomidae each, and a single paper reported Molossidae. There were 3 genera in the Pteropodidae and Vespertilionidae each, 2 in Hipposideridae and Phyllostomidae each, and only a single genus in each the Miniopteridae, Rhinolophidae, Hipposideridae each.

There were 22 Miniopteridae, 610 Pteropodidae, 40, Vespertilionidae, 25 Rhinolophidae, 16 Hipposideridae, 7 Phyllostomidae, and 4 Molossidae bats in the SQLR database.

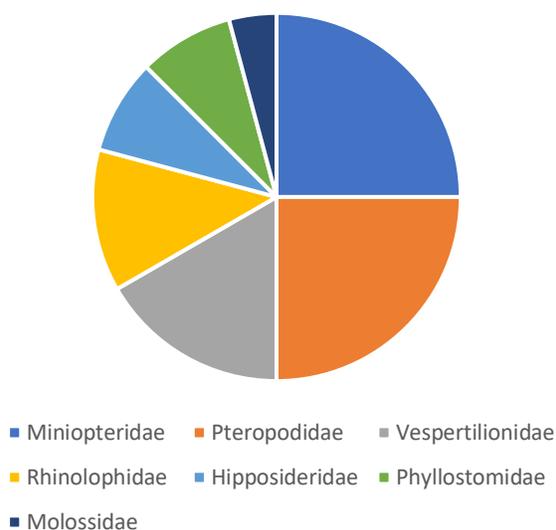


Figure 9: Number of papers which report each family in the SQLR Database

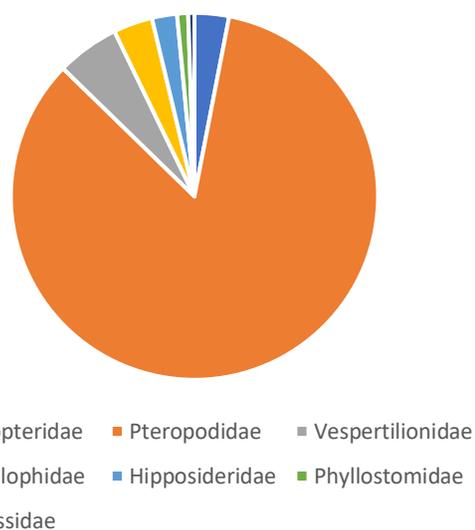


Figure 10: Number of individual bats by family in the SQLR Database

Dependoparvovirus: 5 of the 7 papers reported the family of the bats which had *Dependoparvovirus* infections. Of the papers that reported the families of bats, 4 reported *Dependoparvovirus* infections in only one family of bats, while one reported *Dependoparvovirus* infections in two families. 3 families were reported in the 5 papers, with Rhinolophidae,

Phyllostomidae, and Vespertilionidae each reported in two papers. There were 3 genera in the Vespertilionidae family, 2 genera in the Phyllostomidae family, and 1 genus in the Rhinolophidae.

Astrovirus: All but one paper reported the family of the bats which had viral coinfections. 6 papers reported coinfections in only 1 family of bats, and 1 paper, Mishra et al. 2019 reported coinfection in 2 bat families. A total of 5 families of bats were reported in the 8 papers. Vespertilionidae was reported in 3 papers, Pteropodidae was reported 2 papers, Emballonuridae, Hipposideridae, and Miniopteridae were reported in 1 paper each. There were 2 genera in the Vespertilionidae, and 1 in Miniopteridae, Vespertilionidae, Hipposideridae, Pteropodidae, and Emballonuridae each.

Genera

SQLR: All papers reported the genus of the bats which had viral coinfections. 17 papers reported 1 genus with coinfections. 1 paper reported 3 genera with coinfections and 3 papers reported 2 genera with coinfections. A total of 13 genera were reported in the 21 papers. *Miniopterus* bats were reported in 6 papers, *Rhinolophus* and *Rousettus* bats were reported in 3 papers, *Desmodus*, *Hipposideros*, *Myotis*, and *Pteropus* bats were reported in 2 papers, and *Chaerephor*, *Diphylla*, *Eidolon*, *Nyctalus*, *Otomops*, and *Pipistrellus* were each reported in a single paper. There were 6 species in the *Miniopterus* genus, 2 species in the *Rhinolophus*, *Hipposideros*, and *Myotis* genera each, and 1 species in *Desmodus*, *Diphylla*, *Eidolon*, *Nyctalus*, *Otomops*, *Pipistrellus* genera each. There was 2 identified species reported to have coinfections in the *Rousettus* genus, and another unidentified species in the Yunnan Province of China, 1 identified species in the *Pteropus* genus, with another unidentified in Indonesia, and one study reported coinfections in an unidentified *Chaerephor* bat from Kenya.

Dependoparvovirus: The same 5 papers that reported the family of bats in which they found *Dependoparvovirus* infection reported the genus of the bat in which they found the virus. 3 papers reported 1 genus with *Dependoparvovirus*. 2 papers reported multiple genera, one with 2 genera, and another with 3. A total of 6 genera were reported with *Dependoparvovirus* infections in the 7 papers. *Desmodus*, and *Rhinolophus* were both reported in 2 papers, and *Antrozous*, *Diphylla*, *Myotis*, and *Scotophilus* were each reported in 1 paper. There were 3 species reported in the *Rhinolophus* genus, and 1 species reported in each of the other genera.

Astrovirus: All but one paper reported the genus of the bats which had viral coinfections. 6 papers reported coinfections in only 1 genus of bats, and 1 paper, Mishra et al. reported coinfections in 2 genera of bats. A total of 6 genera were reported in the 8 papers. *Myotis* and *Eidolon* were each reported in 2 papers and *Miniopterus*, *Pipistrellus*, *Hipposideros*, *Taphozous* were reported in 1 paper each. There was no species reported for the *Miniopterus* genus, 2 for *Myotis*, and 1 for each of the other genera.

Species

SQLR: 18 papers reported the species names for which they detected viral coinfection, while 2 papers did not report the species name, and another paper only reported some of their species names. 21 species of bats were reported in the 21 papers. 3 papers reported *Rhinolophus sinicus*, 2 papers reported *Desmodus rotundus*, *Miniopterus schreibersii*, *Miniopterus fuliginosus*, and *Myotis ricketti*, and only a single paper reported *Diphylla ecaudata*, *Eidolon helvum*, *Hipposideros cervinus*, *Hipposideros pomona*, *Miniopterus fuscus*, *Miniopterus griveaud*, *Miniopterus inflatus*, *Miniopterus pusillus*, *Myotis fimbriatus*, *Nyctalus noctula*, *Otomops martiensseni*, *Pipistrellus pipistrellus*, *Pteropus giganteus*, *Rhinolophus affinis*, *Rousettus aegyptiacus*, and *Rousettus leschenaultii* each.

Dependoparvovirus: 5 papers reported the species names in which they detected *Dependoparvovirus*, while 2 did not report the species names. 8 bat species were reported as positive for *Dependoparvovirus* in these 7 papers. *Rhinolophus pusillus*, and *Desmodus rotundus* were reported in 2 papers, and *Rhinolophus sinicus*, *Antrozous pallidus*, *Diphylla ecaudata*, *Myotis davidii*, and *Scotophilus kuhli* were each reported as positive in a single paper.

Astrovirus: 6 papers reported the species for which they detected viral coinfection. 2 papers reported *Eidolon helvum* and *Pipistrellus pygmaeus*, *Myotis mystacinus*, *Myotis fimbriatus*, *Hipposideros cervinus*, and *Taphozous perforatus* were each reported in a single paper.

Discussion:

Searches + Database

Many of the searches, and many of the references of those papers had repeated papers. There were 252 results from my Web of Science searches, and 66 of them were repeats (Table 2). There were also many repeated results between the Scopus and Web of Science Searches, but 4 were added from the Web of Science Searches that were not identified in the Scopus searches (Table 2). In Scopus Search 7 there was paper which came up twice. By limiting my SQLR database to only specific searches I was unable to include several papers that were eligible for inclusion in the database. It is possible that my results from those searches would have been more interesting about the total body of literature, but they would have detracted from my ability to discuss the accessibility of the literature by keyword searches.

The astrovirus database allowed discovery of more papers on astroviruses which reported coinfections. This confirmed the hypothesis that there were many more papers which would not

be picked up by coinfection search terms. With at least 62.5% of astrovirus coinfection papers left undiscovered by the searches, this suggests that there may be as little as a third of the papers which report viral coinfection in the database. This is because of how the papers reported the viral coinfections, incidentally, and their lack of inclusion of coinfection as a keyword in the title, abstract or author keywords on which these searches rely.

The inclusion criteria were strict, and a number of papers were excluded from databases due to slight infractions. Two papers, Lacroix et al. 2017 and Lee et al. 2018 were excluded from the astrovirus database because they refrained from referring to coinfecting viruses as different strains, species or genotypes. Rather, they reported nucleotide % differences, and cited the lack of literature on astroviruses, saying that there is no consensus at this time on what defines different species or strains of astroviruses (Lacroix et al. 2017, Lee et al. 2018). This is one of the difficulties of virology, that as viruses are not alive, the biological species concept, nor any species concept is truly appropriate for these individual viruses. Deciding where the cutoff is for any one operational taxonomic unit (OTU) is difficult, and particularly difficult in virology, where the difference in nucleotide identity required to define different species varies by family (Simmonds and Aiewsakun 2018). Where Lacroix et al. 2017 and Lee et al. 2018 declined to make decisions, the papers with intrafamilial coinfections in my database decided to differentiate between different viruses. Some, like Lau et al. 2010 referred to them only as different genotypes, and refrained from declaring them different species.

Data Extraction

There was much difficulty in determining coinfection in many of the papers. The keywords coinfection, cocirculation, and coexistence were all utilized in the searches, despite only true coinfection being eligible for inclusion in the databases. Where coinfection refers to

two distinct viral OTUs in a single individual bat, cocirculation refers to any two viral OTUs in a population of bats. As such, many papers were ineligible.

Papers reporting coinfection rarely included it as a section of their results. Some included it in text in the body of the results, or just in the discussion. Other papers presented coinfections in tables or figures of the paper. Other papers still included coinfections only in supplemental documents. When it would have only been possible to determine coinfection by extracting the information from a barely legible phylogenetic tree, and then deciphering the names of various viruses via the (only sometimes provided) naming scheme, the task was abandoned, and the paper was discarded as not containing coinfection in a way that was reported.

Coinfection – SQLR Database

Most papers presented only intrafamilial coinfection in a single family, or interfamilial coinfection between 2 different families. Anthony et al. 2013, was a remarkable paper in many ways. It had a dedicated results section on coinfection, and included a table dedicated to intrafamilial coinfection and figure dedicated to interfamilial coinfections. In addition, it reported 588 of 725 coinfections, and thus is responsible for the majority of the coinfection data. That is why, for example, there were so many herpesviruses in intrafamilial coinfections reported, because Anthony et al. 2013 reported 986 of them.

Adenovirus and coronaviruses were reported as having interfamilial coinfections in 5 papers from the SQLR Database. They were also the interfamilial cross with the most coinfections (Figure 2). This suggests that adenoviruses and coronaviruses are some of the most studied viruses in bats.

Coinfection – *Dependoparvovirus* Database

Despite *Dependoparvoviruses* normally requiring coinfection with a large DNA helper virus, only 55/166 were reported as coinfecting. Even in studies such as Li Y. et al. 2010 or Escalera-Zamudio et al. 2018, where every bat sample collected was tested for both *Dependoparvoviruses* and adenoviruses, the ranges of coinfection with adenovirus in *Dependoparvovirus* positive samples were only 19.3% and 33.7% respectively. This suggests that either there is extensive autonomous replication, other helper viruses which were either not detected or not reported, or that there is more complex and unknown dynamics at play in *Dependoparvovirus* infections.

Anthony et al. 2013 reported positive in terms of likelihood of coinfection between particular strains, as well as negative associations in certain intrafamilial herpesvirus coinfections. Some papers reported positive statistical associations of coinfection, indicating that infection with one increases the likelihood of infection with another, such as between astroviruses and coronaviruses in Seltmann et al. 2017. Other papers, such as Chu et al. 2008, reported that there was no such statistical association in the patterns of coinfection between viruses they detected.

There were studies with pooled samples that reported their information in such a way that meant that there must have been a coinfecting individual, but it is impossible to determine what viruses that individual had out of the lot. For example, Yinda et al. 2017 reported viruses from pools of 3-5 individual bats, and some pools had up to 9 viral families detected in a single pool. Now that could be 1 bat with 9 viruses, it could be 5 bats with 100's of viruses within those viral families, but there is no way to know. While it is more economical to test multiple samples at

once, the loss of that coinfection data, which is also important should be a consideration for future research.

The most striking feature of the results from the Geography section of the results is how much of the research is from Asia, and specifically China. More than half of the papers were published in Asia, and of first author affiliation cities, China holds both #1, and a tie for #2 (Figure 5, Figure 6). The original SARS outbreak happened in China, and 8/12 of the papers that reported coinfections of coronaviruses were from China. A particular lack of papers from Australia and South America were also noted. While there was one South American paper in the *Dependoparvovirus* database, there was none in the other databases. Australia has quite a few bats, and is known for its zoonotic Hendra virus, and other bat lyssaviruses. There were papers of Australian origin in the searches, but they were eliminated for pooled samples which made their reported coinfections ineligible for the SQLR database, such as in Peel et al. 2019.

Sample Collection

The most common form of sample collection was fecal. Many studies reported oral swabs as well, and studies reported that while oral swabs were better for detecting herpesviruses, anal or fecal swabs were better for detecting adenoviruses and coronaviruses (Lau et al. 2007, Wray et al. 2016). Due to adenoviruses and coronaviruses being reported in the most number of papers, it makes sense that fecal swabs were the most commonly collected sample if researchers were targeting those viral families.

Sample Processing

PCR was used in every paper in the SQLR database, and metagenomics in only 2, while metagenomics was used in 4 of the papers in the *Dependoparvovirus* and PCR was not used in

all of them. This may be because the papers in the *Dependoparvovirus* database were permitted to use pooled samples, which are likely thought to have more viruses, and thus using metagenomic techniques makes more sense.

Verbiage

Coinfect* was used in the highest percentage of papers in the SQLR database, likely because the papers largely came from searches which included it as a search term (Figure 8). It was found the least in the *Dependoparvovirus* database, which makes sense as it was the only database not required to report a coinfection. Zoon* was interestingly used the most in the astrovirus database, but used at least 80% of the time in each of the databases (Figure 8).

Bats

Pteropodidae tied for first place, being reported in 6 papers, but was easily the family with the highest number of individual bats in the SQLR database (Figure 9, Figure 10). This was because of Anthony et al. the paper which contributed the most coinfection data of any paper to the database.

Some information about the bats was not reported. This was often because the data on coinfection was separated from the rest of the data, and it would be simply reported that there was a coinfection detected. Other times papers were not comfortable identifying the bat down to the species level. In the *Dependoparvovirus* database, there were papers which used pooled guano from multiple species, and in those cases, they were also unable to report which virus had the infection. While the extreme focus on Pteropodidae is not surprising due to their rich viral zoonotic diversity (Anthony et al. 2013), other families of bats may have valuable data to offer on viruses or on coinfections.

There was a greater diversity of species in the Miniopteridae family than any other, with 6 species reported. Miniopteridae was the only family which was reported in 6 papers, and as such it is not surprising that they were the most specious of the families.

Conclusion

There were several trends which appeared in the papers. Papers mostly came out of Asia, and specifically China. They focused on adenoviruses, coronaviruses and herpesviruses, and they focused on them in only a few bat families. Much of the data was reported accessibly, and it seems that as much as 2/3 of the papers reporting viral coinfections are not mentioning coinfection in the title, abstract, or in a keyword. Due to the importance of coinfection dynamics on a number of factors important both for humans and our bat friends, researchers should get better at reporting coinfection in a clear manner, and the research and researchers should diversify.

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Appendix 1:

SQLR Database:

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