

Original Contribution

Zoos as Sentinels? A Meta-Analysis of Seroprevalence of Terrestrial Mammalian Viruses in Zoos

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Abstract: The One Health framework links animal, human, and environmental health, and focuses on emerging zoonotic pathogens. Understanding the interface between wildlife and human activity is critical due to the unpredictable nature of spillover of zoonotic pathogens from animals to humans. Zoos are important partners in One Health because of their contributions to education, conservation, and animal health monitoring. In addition, the housing of wildlife in captive and semi-natural settings makes zoos, especially relevant for detecting animal-related pathogens. A first step to determine the utility of zoos in contributing to pathogen surveillance is to survey the peer-reviewed literature. We, therefore, retrieved data from the previous 20 years and performed a meta-analysis to determine global patterns of viral seroprevalence in mammals housed in zoo collections from peer-reviewed literature. We analysed 50 articles, representing a total of 11,300 terrestrial mammals. Increased prevalence was found in viruses strictly targeting specific host taxonomy, especially in viruses transmitted through direct contact. Potentially complex patterns with geography were also identified, despite uneven sampling. This research highlights the role zoos could play in public health and encourages future standardized epidemiological surveillance of zoological collections.

Keywords: Virus, Seroprevalence, Meta-analysis, Zoos, Terrestrial mammals, One health, Captivity, Epidemiology

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INTRODUCTION

It is estimated that 60% of new infections that affect humans have a zoonotic origin (Karesh et al. 2012). For example, outbreaks of Ebola, West Nile (WNV), and Severe Acute Respiratory Syndrome (SARS) associated viruses are linked to animal reservoirs (Rabozzi et al. 2012). Because the emergence and transmission of zoonotic viruses are often unpredictable, and non-zoonotic viruses can also be

detrimental to the ecosystem, understanding the interface between wildlife, pathogens, and human health is critical (Pulliam et al. 2012; Rabozzi et al. 2012). One Health is a framework that uses an interdisciplinary approach to link human health with that of animals and the environment (Rabozzi et al. 2012; Narrod et al. 2012; Atlas and Maloy, 2014).

Pathogens can affect livestock, leading to billions of dollars in global economic damage (Narrod et al., 2012; Pendell et al. 2014; Munnink et al. 2021). For example, bovine spongiform encephalitis, SARS, influenza A H1N1 and Highly Pathogenic Avian Influenza (HPAI) have led to an estimated \$220 billion in losses globally (Pendell et al. 2014). Wildlife populations are also susceptible to outbreaks of pathogens that may accelerate species decline and the risk of extirpation (Earl et al. 2016). Because human, animal and environmental health are inextricably linked, threats to animals and the environment are also a concern for human health (Everard et al. 2020; Austin 2021).

Zoological facilities (including zoos, aquariums, wildlife parks, nature centres, sanctuaries and research facilities—henceforth zoos) provide the opportunity to further the One Health framework. Zoos are integral to public education and provide roughly 350 millions (USD) in global funds to conservation projects (Gusset and Dick 2011; Mellish et al. 2019). Zoos can also monitor disease transmission at an individual level within their facility (Caballero-Gomez et al. 2019, 2021) and may provide greater insight into animal populations at the human-animal interface (Robinette et al. 2017). Infectious diseases often remain the most common cause of mortality in zoo animals (Scaglione et al. 2019). Finally, zoo animals may be exposed to pathogens between conspecifics or across species, and they can be tested in a reasonably controlled environment to survey for antibodies (Huang et al. 2009; Greenwood et al. 2012; Cano-Terriza et al. 2015).

Spatial and temporal factors can affect the prevalence of pathogens in zoos. For example, host species diversity can influence pathogen spread, so zoos with more diverse species or that are in biodiversity hotspots may be affected differently than zoos with fewer species (Ostfeld and Keesing, 2012). Moreover, housing a species in a zoo outside of its natural range may increase exposure to novel pathogens (Bartlett et al. 1984; Cunningham 1996). Pathogen transmission can also change over time, and human activity has been shown to increase disease transmission (Waits et al. 2018; Fouque and Reeder 2019; White and Razgour 2020). It may also be the case that recent outbreaks

and the increased application of One Health have increased the detection of viral prevalence in zoo animals.

Given the interest by One Health on the potential use of zoos as epidemiological monitoring stations (McNamara 2007; Robinette et al. 2017), and the importance of understanding the prevalence of pathogens for human and wildlife health, we argue that it is critical to investigate the prevalence of pathogens in zoo collections. Therefore, we used published literature on viral seroprevalence to evaluate global patterns of viral disease prevalence in terrestrial mammals that have been reported in zoo collections. We considered three moderator groupings to summarize trends: host-related, virus-related, and publication-related. By understanding patterns of disease reporting from zoos we can begin to attune epidemiological research and further advance knowledge gained through One Health. Moreover, we can address limitations in sampling efforts in zoos that may be key in identifying and monitoring diseases in the future. We predicted that (1) animals housed outside their home range would exhibit higher seroprevalence, (2) zoos with greater single-species collection would have more species-specific seropositivity, and (3) host taxonomy will affect variation in seropositivity in well-studied viruses.

METHODS

Data Extraction

To quantify viral seroprevalence in zoo mammal collections, we conducted a literature search from 2001 to 2021 using Google Scholar and OMNI databases. Search terms included “zoo”, “mammal”, “virus”, “captive*”, and “seroprevalence”. Papers were assessed for relevance based on the full text to ascertain whether the study met the criteria listed in Figure S1, using ELISA tests only. The following data were extracted from each accepted article: year of publication, first and last year of data collection, host population parameters: location of natural habitat (country and continent), and location of the captive population (continent), type of captive facility, host taxonomy, host IUCN status (as of 2021), sample size, number of asymptomatic seropositive animals for each virus, and virus taxonomy. For each virus species, mode of transmission was documented, and zoonotic potential was defined as positive if there is a cytopathic effect on human cells documented in the scientific literature as of 2021.

Meta-Analysis of Data

In this study, the prevalence of viral infections was estimated as a ratio of seropositive samples to the total sample size for each host species in each zoo location. Data were grouped for statistical analysis based on host species, virus tested, and zoo location from each publication. Therefore, if a study evaluated multiple taxa, a single study could yield multiple groups to be included in the meta-analysis. All data analysis was conducted in R v.4.0.3 (R Core Team, 2021). An overall test for heterogeneity was conducted to inspect publication bias, as well as a funnel and Egger's test for funnel asymmetry. The Cochran's Chi-squared test (Q test), Tau^2 , and Higgin's index (I^2) were used to measure heterogeneities in the overall dataset and for group analyses. I^2 estimates greater than 75% were considered as high heterogeneities (Wang, 2016).

Random-effects model estimations with restricted maximum likelihood method were used to explain the heterogeneity of seropositivity in different moderators through double arcsine transformation of seroprevalence effect sizes using the *metafor* package (V3.0–2, Viechtbauer, 2021). The following moderators were inspected separately: (1) publication-related moderators (year of publication, length of study, sample size classes, number of facility by study), (2) host-related moderators (zoo continent location, facility type, taxonomy, IUCN status), (3) virus-related moderators (zoonotic potential, type of transmission, taxonomy), (4) host and viral taxonomy moderators (interaction of host and viral taxonomy). We only considered taxa for host and viral taxonomy with a total sample size across studies greater than 30. Within study variation was assumed to be different between moderators and double arcsine estimates were backtransformed to seroprevalence estimates. Each moderator was evaluated separately in univariate models before being tested simultaneously in a single meta-regression model when significant in univariate models. Significance level was set as $\alpha < 0.01$.

RESULTS

Literature Search

A total of 6,020 articles were identified within local and international databases, including Omni (a database hosted by Queen's University, Ontario Canada, that connects

journal subscriptions among Ontario post-graduate institutions, $n = 403$ articles) and Google Scholar ($n = 5617$ articles) from January 2000 to December 2021 (Figure S1). After review based on title, abstract, and full text, 50 articles were accepted, including 1036 grouped data, representing a total of 11,300 terrestrial mammals tested for viral seroprevalence in zoos. The 50 retrieved articles reported seropositivity from all seven classes of viruses from the Baltimore classification on a total of 12 mammalian orders and 302 facilities (Fig. 1, S1&S2). None of the animals tested had specific vaccination history related to the pathogens investigated.

Overall Heterogeneity Assessment and Publication Bias

Heterogeneity in seropositivity effect sizes was identified and quantified in the entire dataset. The overall estimate of seroprevalence in all species combined was 5.41% (95% CI = 3.86–7.14%). Great overall heterogeneity was observed ($\text{Tau}^2 = 0.0629$; SE = 0.0049; $I^2 = 73.94\%$), with significant variation in seropositivity between studies ($Q = 5858.67$, $p < 0.0001$). In the analysis of publication bias, a non-significant asymmetry of the funnel plot was noted for seropositivity frequency among all captive terrestrial mammals held in captive settings (Figure S3; Egger's test: $t = -0.5266$, $p = 0.5986$).

Moderator Analysis

Publication-Related Moderators

When considering sample size classes (< 5, 5–10, 10–50, and > 50 animals tested), moderator differences for estimates variation in seroprevalence were significant ($Q = 28.56$, $p < 0.0001$) with great heterogeneity ($I^2 = 82.3\%$). Higher seroprevalence was observed when the sample size was greater than 10 individuals per species for each virus tested (Table S1A). Year of article publication was not a significant predictor of seroprevalence heterogeneity within the dataset ($F = 2.47$, $p = 0.117$), nor was number of facility by study ($F = 0.166$, $p = 0.683$). The duration of sample collection accounted for 4.74% for variation ($F = 37.9$, $p < 0.0001$; $I^2 = 67.76\%$; Table S1A) and had a weak negative effect (estimate = -0.0081 ; SE = 0.00132; $p < 0.0001$).

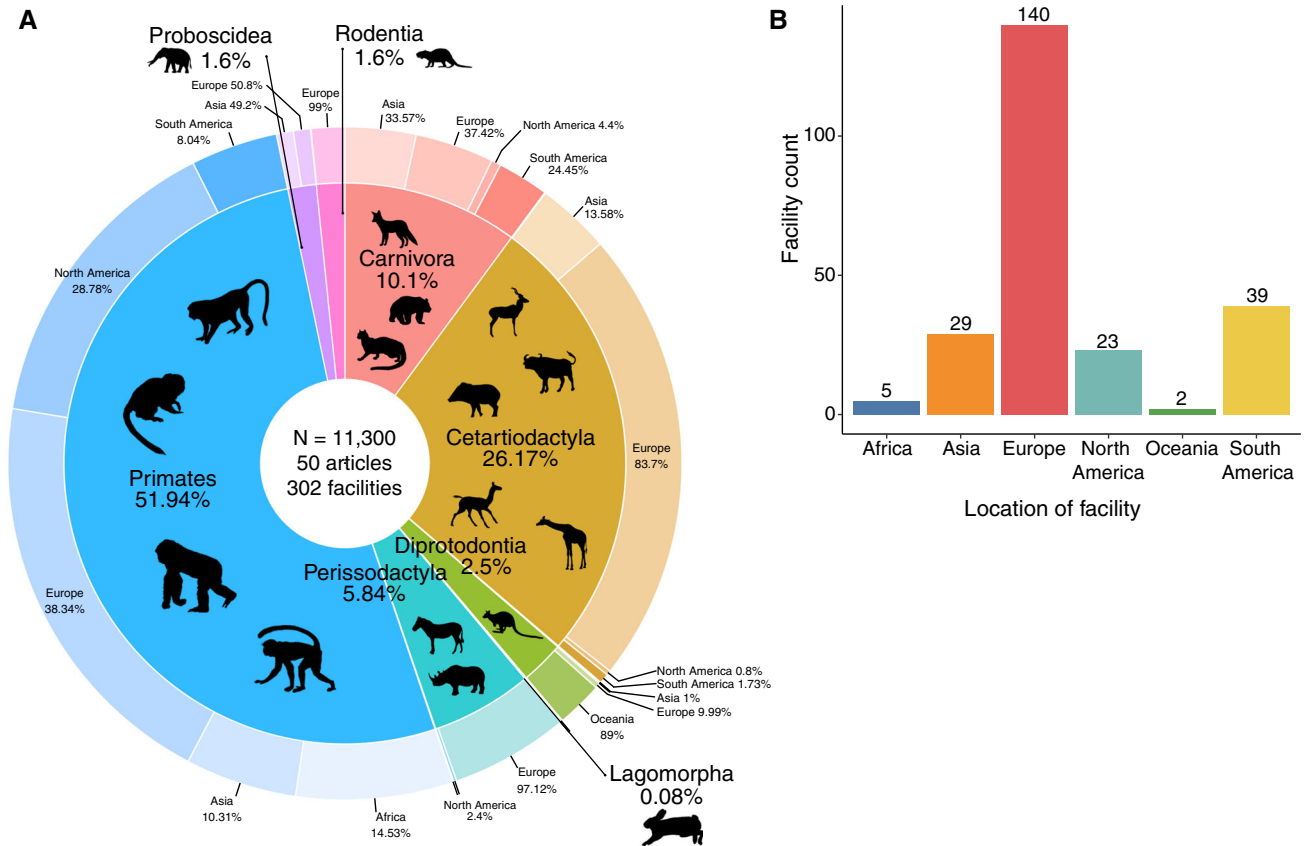


Figure 1. **A** Pie chart of sampling dataset extracted from the literature search, according to host taxonomy and the location of their captive facility. Only most representative taxa are shown. **B** Bar plot of number of facilities included in the meta-analysis according to continent.

Host-Related Moderators

The type of captive facility did not have a significant effect on seropositivity heterogeneity ($Q = 4.6$, $p = 0.0321$, Table S1B). Animals hosted outside of their distribution range at the continent level had no significantly greater seropositivity prevalence ($Q = 6.12$, $p = 0.013$) than animals held in zoos within their natural range. However, large heterogeneity within location moderators remains (outside: $I^2 = 84.6\%$; within: $I^2 = 81\%$). Seroprevalence significantly varied according to each continent the zoo was located in ($Q = 49.73$, $p < 0.0001$; Fig. 2), with greater seroprevalence in North and South American facilities (20.93% and 20.1%, respectively), the lowest in African facilities (0.7%). No significant differences in seroprevalence were detected in the IUCN conservation status among hosts ($Q = 5.89$, $p = 0.317$, Table S1B).

Moderator differences for estimated variation in seroprevalence were significant according to host order

($Q = 73.9$, $p < 0.0001$). The order that had the greatest seropositivity (54.9%) was Proboscidea with large heterogeneity ($I^2 = 84\%$; Table S1B), only represented by the *Elephantidae* family. The Lagomorpha and Primates followed with estimates of seropositivity at 12.3% and 8.53%, respectively. Orders with significant Q tests were investigated at the family level ($n > 30$).

Moderator differences were also significantly observed at the host family level ($Q = 239.99$, $p < 0.0001$). Within the order Carnivora, only the families *Felidae* and *Canidae*, had seroprevalence values above 0% (6.4%, 15.6%), and both had significant moderator heterogeneities (86%, 56%). Among Cetartiodactyla, *Bovidae* and *Cervidae* had the highest seroprevalence (5.5% and 5%) and significant heterogeneity ($> 70\%$), but remain at lower seroprevalence than *Equidae* and *Rhinocerotidae* from the Perissodactyla order (5.2%, 11.2%). For Primates, the *Atelidae* and *Cebidae* families had the greatest seroprevalence (59% and 41%) with great heterogeneity. The Primate family with the

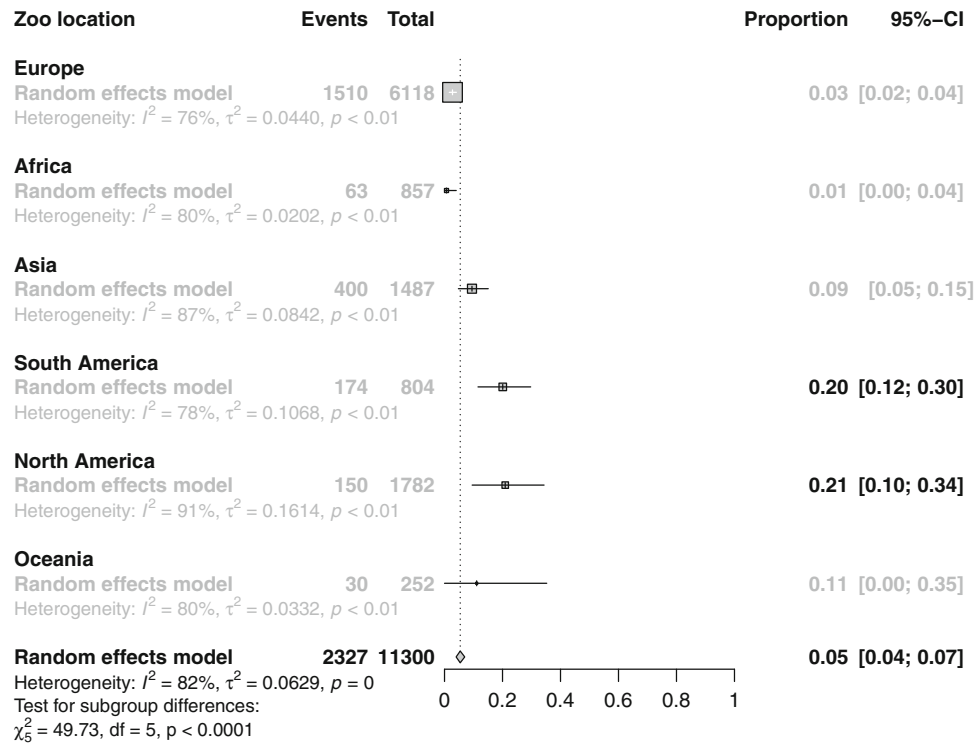


Figure 2. Forest plot of studies for viral seropositivity in captive terrestrial mammals according to zoo geography by continent. Random-effects estimate (DerSimonian and Laird method).

greatest heterogeneity was *Atelidae* (seroprevalence: 3.4%, $I^2 = 93.8\%$).

Virus-Related Moderators

Viruses considered zoonotic agents had no significant differences in seroprevalence than non-zoonotic agents ($Q = 1.43$, $p = 0.2321$, Table S1C). Moreover, greater seroprevalence was observed for pathogens transmitted through direct contact than through arthropod vectors (9.42% and 3.1%, respectively; $Q = 120.8$, $p < 0.0001$). Notably, viruses with currently unknown transmission types had the greatest seroprevalence within the dataset (47.81%). When investigating viral taxonomy from the Baltimore classification angle, all animals tested for the only single-stranded DNA virus (Class-II, Feline parvovirus) were seropositive. On the other hand, the virus species with the greatest prevalence for class-I was the Elephant Endotheliotropic Herpesvirus (EEHV, 85.8%), followed by the Simian virus 40 (47.81%), and the Cervid herpesvirus (20.34%). Finally, 38.27% of the animals tested for the Simian foamy virus, within the class-VI were seropositive (Table S1C).

Meta-Regression Analysis

Overall Model

In the multivariable analysis, 11.08% of the total heterogeneity in the dataset was accounted for, and moderator differences in seropositivity were significant ($F = 5.0744$, $p < 0.0001$, $I^2 = 62.51\%$). Based on our model, the average seropositivity in a zoo population is 28% (SE = 14%; Table S2A). Sample size impacted seropositivity, with especially large effect sizes when more than 50 individuals or lower than five were sampled within a study. Seroprevalence was generally higher for hosts held in North American zoos outside of their distribution range (Table S2A).

Host and Viral Taxonomy Moderators

To investigate the taxonomic depth of the host reservoir for viral seroprevalence a meta-regression was conducted, including both host taxonomy at the order level ($n > 30$ families) and viral class. Within-moderators differences were significant ($F = 6.143$, $p < 0.0001$, $\text{Tau}^2 = 0.0628$, $I^2 = 71.92\%$) and accounted for 39.3% of the heterogeneity

between studies. *Canidae* and *Felidae* were more significantly seropositive for class-IV viruses, with greater infection to WNV in the dataset (Table S2B; Figs. 3 & S4). *Felidae* had significantly increased prevalence to class-II

viruses because all animals tested were positive for the feline parvovirus (Table S2B). Elephants were highly infected by EEHV (79% ± 14%) belonging to class-I, the Blue-tongue virus, only representative of class-III (58% ± 22%)

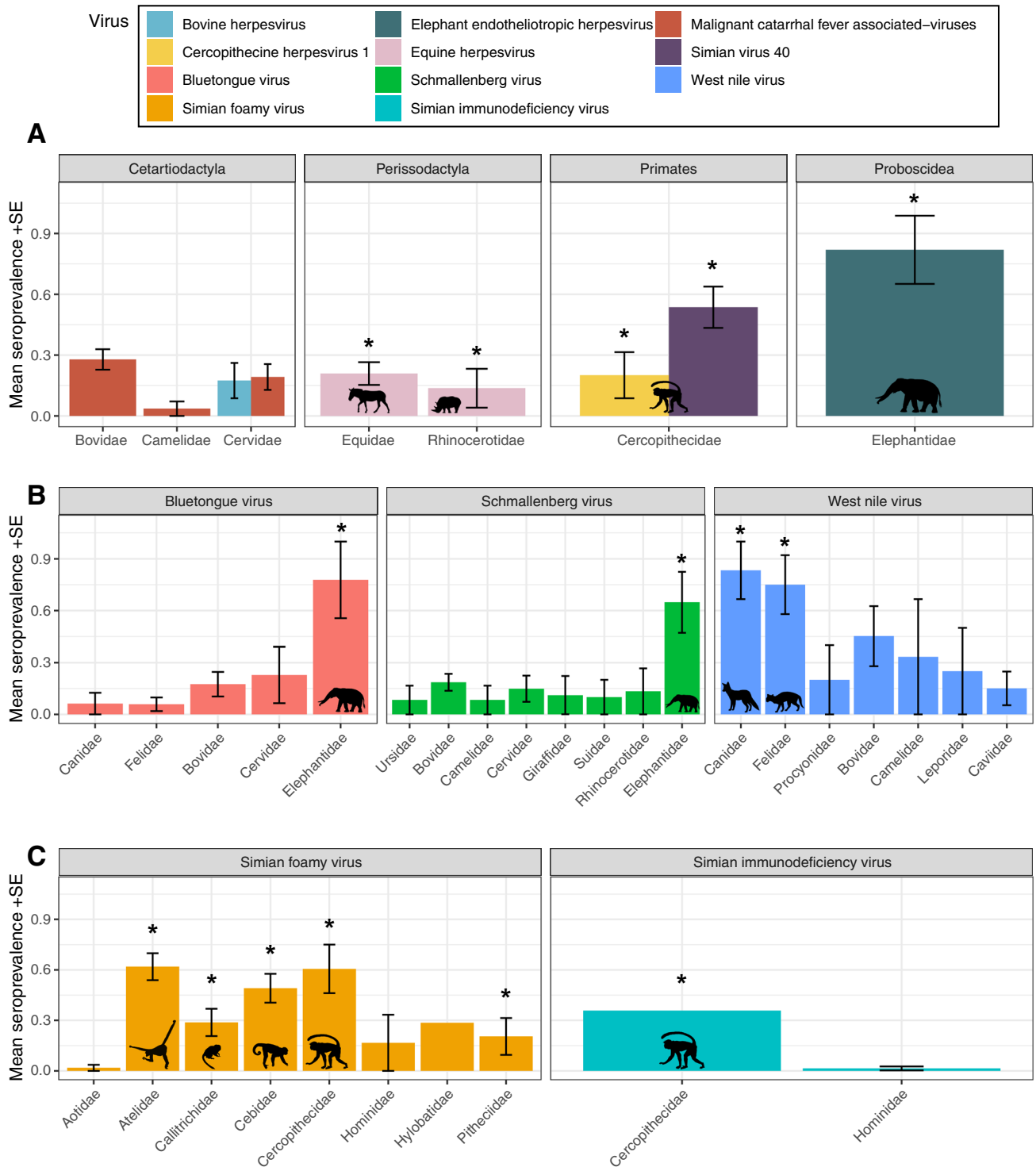


Figure 3. Mean seroprevalence for specific virus investigated according to host taxa of interest. Asterisks represent significance according to the model (see Table S2).

as well as the Schmallenberg virus ($48\% \pm 17\%$). *Herpesviridae* such as the Equine herpesvirus was also highly prevalent in Perissodactyla ($19\% \pm 6\%$). Finally, class-VI viruses infected most of the Primate order, represented by the Simian foamy virus and Simian immunodeficiency virus ($23\% \pm 6\%$), as well as class-I Simian 40 virus and Cercopithecine herpesvirus in *Cercopithecidae* ($28\% \pm 8\%$).

DISCUSSION

An important consideration to interpreting our results is that the data reviewed in this analysis are not a random sampling of all animals in zoos, and only articles performing ELISA methods for antibody detection were included. We recognize each study would have their own motivations for testing which introduces inherent biases of these results. This does, however, provide us the opportunity to identify these biases and report trends in the literature which will be crucial to prove the utility of zoos as sentinels of disease.

Given the temporal scope of this study, publication-related moderators were assessed to account for changes relating to time and publication-specific variation. We found significantly higher seroprevalence detection rates in studies with a sample size greater than ten conspecifics. This result may be explained by greater transmission through enclosures with a high number of conspecifics. Zoos rarely hold more than ten *Elephantidae* or *Felidae* of the same species, but social taxa such as Primates and *Cervidae* are usually held in larger groups. While group size is a key determinant for social and reproductive behaviours in captivity, there is some flexibility in group size for many species depending on the evolutionary origin of sociality (Price and Stoinski, 2007). As this information was not documented in the literature included in our analysis, examination of those details could shed light on this trend.

The relationships between geography and viral presence, prevalence, and spread have long been investigated in human and animal systems (Hjelle et al. 1995; Munster et al. 2007; Abubakar et al. 2009; Han et al. 2016). This framework is particularly relevant for animals housed outside their natural geographic range, where they can be exposed to novel pathogens. However, our results did not reveal differences in seropositivity between animals housed within and outside the continent of their natural range. The absence of pattern could be explained by similar prophylaxis and disease management plans among facilities. For

example, the Transmissible Diseases Handbook, compiled by the European Association of Zoos and Wildlife Veterinarians' Infectious Diseases Working Group (IDWG) offers guidelines on many diseases that are freely available worldwide. Similarly, related species within a zoo can be administered the same vaccines, medications, and sanitary measures irrespective of the species geographic origin. Restrictions in the data also meant that this analysis was performed at the continent level without taking into account cultural differences in veterinary practices, and differences may be detected at a finer scale.

While zoos in Europe had the highest overall sampling effort, North American zoos were sampled in only five articles within our criteria, suggesting that high seropositivity rates can be an artefact of disproportionate sampling. However, zoos in North America tend to have higher species diversity than those in Africa, Asia, Australasia, and Europe (Brereton and Brereton 2020). As WNV was one virus tested in these studies, it is possible that increasing diversity of hosts likewise increases the probability of encountering this virus, since it can infect many species. There is evidence suggesting that increasing host species diversity can increase disease prevalence (Keesing et al. 2006), which may result in higher seropositivity rates in species-rich North American zoos. However, the relationship between species diversity and disease risk is highly dependent on the transmission method, virulence, and more importantly study systems and testing occurrence (Keesing et al. 2006). Moreover, the Simian foamy virus was also extensively tested in American zoos, which is known to be naturally present in many Primates and has limited health consequences to date (Pinto-Santini et al. 2017).

We found the highest overall seropositivity for species in highly represented taxa in zoo collections. These taxa are well-studied as they are considered visitor favourites (sometimes referred to as charismatic animals, Carr 2016; Albert et al. 2018). Increased prevalence in viruses targeting specific hosts was found such as Equine herpesvirus in Perissodactyla. High seropositivity of EEHV within multiple articles was also identified, as well as high seropositivity in elephants for the Bluetongue virus and Schmallenberg virus, especially considering that *Elephantidae* represented 1.6% of the dataset. The high seropositivity found for Bluetongue virus was suggested to occur from outbreaks from free-ranging wildlife or livestock surrounding the zoo (Dowgier et al. 2018, Caballero-Gomez et al. 2021). In the same way, increased seroprevalence of WNV was found for

captive *Canidae* and *Felidae*, a possible consequence of the role of various peridomestic mesocarnivores in WNV amplification cycles (Root, 2013). For EEHV, the virus can be naturally present in free-ranging elephant populations, but is the most common cause of death in Western captive elephant populations globally over the last few decades (including *E. maximus*, but also *E. loxodonta*; Hoornweg and Schaftenaar 2021). Detection methods for EEHV have improved over time, and further research is required to understand the process of virus activation and tools for prevention. Thus, viral transmission must be monitored at a larger scale to limit disease spread.

Our results showed that transmission through direct contact yields more seropositive animals than other transmission types. Because captive animals are held in enclosures that are often more densely populated compared to free-ranging conspecifics, increased transmission rates may occur between co-housed susceptible species. We also observed high seroprevalence for viruses with currently unknown transmission type, mainly from the Simian virus 40. However, since the discovery of animal viral particles from the foot and mouth disease virus in 1898, the number of virus discoveries and available genomes continues to grow (Gibb et al. 2022) and so is our knowledge and prevention of viral diseases. Despite not finding significant difference in seroprevalence between zoonotic and non-zoonotic viruses, the close contact between humans and collection animals in zoos, and the potential for spillover events, remains a key area for future study. Transmission of infectious diseases from zoo animals to workers has been identified in the past (Sandstrom et al. 2000; Cadar et al. 2021), as well as from workers to animals (McAloose et al. 2020), highlighting an area of research worth further investigation.

RECOMMENDATIONS

We have identified trends in seroprevalence of viral diseases in zoos with sample size, location, and between host taxa, which can inform recommendations to improve the feasibility of using zoos as sentinels for disease monitoring. These recommendations reflect the limitations we have seen in this literature search.

- (1) Our results support established research that has identified preference in the scientific literature on zoo collections for well-represented, charismatic mammals

that are typically considered visitor favourites (Carr 2016; Albert et al. 2018). It may be the case that this preference is indirectly motivating health research on these animals given their popularity. Therefore, we recommend that zoos should increase sampling effort to include less-charismatic species to develop a more comprehensive understanding of disease prevalence in these institutions.

- (2) To fully understand the interconnectivity of zoos and surrounding wildlife we suggest more studies should evaluate the seroprevalence of free-ranging and domestic animals in zoo areas due to the bidirectional nature of disease transmission. This will be an important link to monitor disease spread outside the zoo, and possible transmission to humans.
- (3) We suggest increasing public availability of data to increase understanding and prevent transmission and outbreaks. New discoveries of viruses have been increasing rapidly and our understanding of viral systems is still expanding (ICTV Executive Committee 2020). Without further improvements on reporting and availability of data on viral diseases, we cannot use zoos as sentinels to their full potential.

These recommendations can promote the potential role of zoos as sentinels of infectious diseases monitoring and assist zoos in providing crucial information to further understand prevalence and transmission while also acting as an early warning system for disease spread.

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DATA AVAILABILITY

The datasets and Rscript generated and analysed during the current study are available in the metavirzoo repository, <https://github.com/pvanleeu/metavirzoo.git>

DECLARATIONS

CONFLICT OF INTEREST The authors declare that they have no conflict of interest. This article does not

contain any studies with human participants or animals performed by any of the authors.

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