Global patterns of ranavirus detections

Ranaviruses are emerging pathogens of poikilothermic vertebrates. In 2015 the Global Ranavirus Reporting System (GRRS) was established as a centralized, open access, online database for reports of the presence (and absence) of ranavirus around the globe. The GRRS has multiple data layers (e.g., location, date, host(s) species, and methods of detection) of use to those studying the epidemiology, ecology, and evolution of this group of viruses. Here we summarize the temporal, spatial, diagnostic, and host-taxonomic patterns of ranavirus reports in the GRRS. The number, distribution, and host diversity of ranavirus reports have increased dramatically since the mid 1990s, presumably in response to increased interest in ranaviruses and the conservation of their hosts, but also the availability of molecular diagnostics. Yet there are clear geographic and taxonomic biases among the reports. We encourage ranavirus researchers to add their studies to the portal because such collation can provide collaborative opportunities and unique insights to our developing knowledge of this pathogen and the emerging infectious disease that it causes.

Keywords: *Ranavirus*, database, distribution, host range

The Global Ranavirus Reporting System

The Global Ranavirus Reporting System (GRRS; https://brunnerlab.shinyapps.io/GRRS_Interactive/) was designed as a central, open-access, online database in which to report and track the occurrence of ranavirus presence or absence around the world (Duffus and Olson, 2011). Globally compiled detections and non-detections of ranaviruses can provide novel insights into pathogen emergence, host range, and susceptibility. In addition to occurrences, the GRRS is an archive of ranavirus field and diagnostic studies which include additional project aims and details such as detection methods.

Since its initiation in 2015 we have been working to populate the database with records of ranavirus detections. We have focused our efforts on published accounts of ranavirus occurrence, although the GRRS also includes dissertations, seminars, and unpublished accounts, and more are welcome. As of this writing there are 206 studies or publications in the GRRS that provide data on the occurrence of ranaviruses in one or more taxa (Figure 1). This is, of course, a fraction of publications on ranaviruses more broadly (e.g., phylogenetics, experimental studies; see Blaustein et al., 2018 for a review of experimental studies) and, we expect, is far from inclusive of all location or occurrence data hiding in field records and on laboratory computers. One goal of this note is to encourage the broader community to add their unpublished reports of ranavirus to the GRRS. Another is to ask researchers to find their references and offer corrections or refinements to the information in the database. We therefore begin by describing the data in the GRRS and noting some common issues that are likely to be important for those using the GRRS for various analyses.

The GRRS represents a unique tool for researchers and policy makers. Whereas prior publications have described, for instance, the taxonomic breadth of ranavirus hosts (Duffus et al., 2015), the data in the GRRS system provide additional context and facilitate

additional analyses. In particular, the GRRS offers a broad geographic and temporal perspective on the occurrence of ranaviruses and the settings in which ranaviruses have been found. We therefore highlight several interesting patterns in the reports in the GRRS and suggest possible interpretations and hypotheses. We hope that these will inspire further research and more reporting with greater precision.

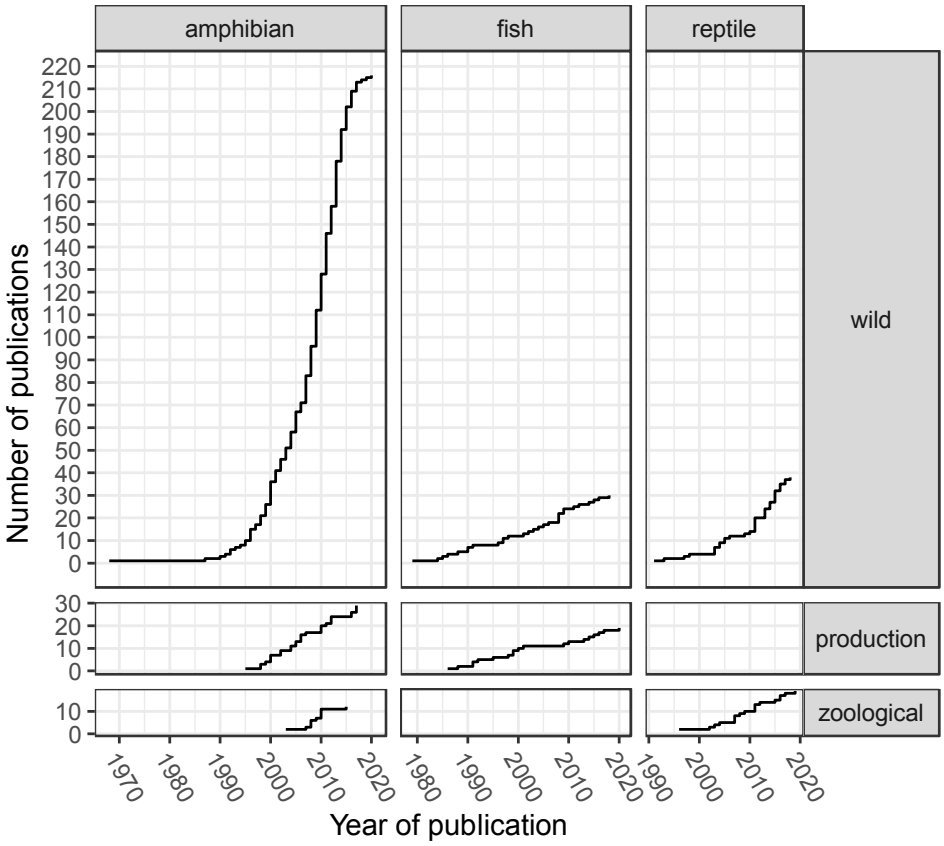

Figure 1: Publications in the GRRS describing ranavirus in each host class from the wild, production (e.g., ranaculture or aquaculture), or a zoological setting. Bars represent publications in each year while the lines are the cumulative total of publications in each category.

Data in the GRRS

The GRRS includes information on the location and date of sample collection; species, life stages, and type of population sampled (i.e., wild, production, or zoological); and information on the numbers of samples screened for infection, confirmed infected, confirmed diseased if relevant, and the type of diagnostic methods employed. Samples include both animal tissues (e.g., liver or tail clip) as well as swabs. They do not yet include environmental DNA or other samples not clearly linked to an individual host. When DNA sequencing data had been submitted to GenBank, the accession number is also included. Each record includes the publication's title, journal or reporting outlet, volume, and pages

(or contact information for unpublished records) so that a user may trace records back to the original publication or source. See the GRRS site for additional metadata.

The data in the GRRS are presented as an interactive map, where clicking on a record (one row in the database is one dot on the map) provides more information about that record. The map can be zoomed and moved. The records are subsettable by population type and taxa. All data can be freely downloaded. The database is organized so that each row represents a unique combination of location, date, or species from a study, where these information were available. Thus a single publication may be represented in the database by one or a series of rows (and points on the map). Again, the database includes both detections and non-detections; both show up on the map. All but seven publications, however, include at least one detection and just 41% of all records are non-detections.

While the GRRS represents a uniquely comprehensive database on the host and geographic distribution of ranaviruses, it is important to note a few important limitations to the underlying records and how we dealt with them. These limitations stem, in large measure, from the fact that many publications in the GRRS focus on the biology of ranaviruses and their hosts (e.g., virology, phylogenetics, conservation) rather than on populating a database of occurrences. We hope, however, that readers will consider consider that their publications may be used in unexpected ways and thus provide greater detail about their collections and results in the future. We also encourage readers to contact us to improve or correct our best guesses for those publications already in the GRRS.

One common issue was simply vague descriptions of the locations or timing of sample collections. For instance, the virus that became the type species of *Ranavirus*, *Frog virus 3* (FV3), was described as coming from "Wisconsin-Minnesota frogs," *Rana pipiens*, in Granoff et al. (1965) and as "derived from an inclusion-containing Wisconsin Lucke tumor" in Rafferty (1965), presumably from a biological supplier collecting from the wild, and neither provided a date of collection. In cases with vague location information we used the midpoint or centroid (e.g., of the state of Wisconsin) or the nearest mentioned landmark (e.g., a city) as the location. When dates were not provided we have used January 1st of the year of publication and when only a month or season was provided we have done or best to find a reasonable midpoint. Note that missing location and temporal data were especially common in earlier records, but also, and perhaps intentionally, in records from production facilities. Other reports, especially those with a more ecological focus, often provide great detail on locations, dates, and numbers. Hence the degree of accuracy and precision in location data in the GRRS is quite variable.

Descriptions of locations for imported animals offer unique challenges; should we use the source's or importer's location? In some cases the source was much less clear than the destination (e.g., reptiles imported into Germany from "Asia") and so we would use the more precise location. In other cases (e.g., the case of newts imported into Germany from a specific location in Iraq; Stöhr et al., 2013) we were able to use the location of the source, at least when the event or detection was recent (within weeks to a few months) of importation. When animals were maintained in a facility for longer periods we would consider this facility the location of record (e.g., as part of a collection or for research; Stöhr et al., 2013).

Second, some care is also required in interpreting taxonomic designations of hosts as nomenclature has changed and, especially for some amphibians, remains contentious. We have left species epithets as written or provided in the publication, but also provided a "translation" to a common set of names of genera so that a single species is not counted multiple times (e.g., *Lithobates* –> *Rana*).

It is also important to note that taxonomy of the genus *Ranavirus*, and indeed the family *Iridoviridae*, has advanced a great deal in the last decade. For instance, the GRRS originally listed five species—FV3, *Ambystoma tigrinum virus*, *Bohle iridovirus virus* (BIV), *European catfish virus* (ECV), and *Santee-Couper virus* as well as "other"—which was current as of 2015, but the latest taxonomic revision removes BIV and ECV and adds *Singapore grouper iridovirus* and *Common midwife toad virus* (ICTV, 2020). Some manuscripts also propose new ranavirus species (e.g., European North Atlantic Ranavirus; (Stagg et al., 2020)). Moreover, the evidence used for species designations has changed over the years (e.g., from restriction fragment length profiles to sequences of portions of key genes to whole genome sequencing). We therefore simply list species as identified in the publication and encourage users interested in ranavirus species designations to review the original papers.

We have also attempted to record the type of population from which samples were collected, although this sometimes involves a degree of interpretation. For instance we have designated the original records of FV3 as having come from the wild, even though the animals were obtained from a biological supplier, as we know suppliers tended to collect from the wild and this designation seemed more appropriate than a production setting (e.g., a ranaculture facility). For some taxa the distinction between wild and production settings is in the eye of the beholder (e.g., the Chinese giant salamander, *Andrias davidianus*, or American bullfrogs, *Lithobates catesbeianus*, that are "ranched" in constructed or semi-natural ponds intended for production, but essentially unmanaged and open to immigration or emigration). In general, "production" was interpreted as being raised or held with the intent of distribution. "Zoological" populations include zoos, private collections, and research populations or colonies not intended for distribution.

Users should be cautious interpreting data on the number of individuals involved or tested. Often this information was simply not provided, at least in a way that can be easily parsed. Perhaps more importantly, different types of research involve very different intensities of sampling (e.g., virus identification from one or a few carcasses vs. a broad epidemiological survey with hundreds of samples). We therefore avoid making comparisons in this manuscript about the impact of ranavirus or number of animals involved in different settings or taxa.

Lastly, it is important to note that the GRRS is not associated with the OIE (World Organization for Animal Health), which lists ranavirus as notifiable diseases (Schloegel et al., 2010). Uploading records to the GRRS does not satisfy OIE and national reporting practices for notifiable infections. Please refer to the reporting rules of the country in which you work and see the OIE's World Animal Health Information System (OIE, 2020).

Patterns in reporting

Since the original publications by Granoff et al. (1965) and Rafferty (1965) describing FV3 isolated from wild amphibians, ranavirus reports were rare for decades. Only in the late 1990s did the number of reports begin to grow substantially (Figure 1). Overall there are far more reports from amphibians than fish and reptiles, and from the wild than production or zoological settings. To a large degree this probably reflects an increased interest in amphibian diseases as threats contributing to global declines in amphibian populations (Daszak et al., 1999). Indeed, the increase in reports from amphibians in the GRRS mirrors an overall increase in publications about amphibian pathogens (Blaustein et al., 2018). Moreover, most reports from the mid 1980s through the early 2000s focused on mortality events, although there has been a clear trend towards routine screening in wild populations in recent years (Figure 2). To the extent that ranaviruses were found in fish and reptiles in the wild, it tended to be in sport fish in recreation sites and turtles in reserves.

Reports in production and zoological settings tended to stem from mortality events rather than routine screening (Fig. 2). Reports from amphibians in production settings included bullfrogs, *Rana catesbeiana* (n=7 publications), but also single records from other ranids and two salamanders. Interestingly, there are no current GRRS reports of reptiles in production settings. Reports from fish in production settings were limited to single instances per species. Surprisingly there was only one instance of a ranavirus from fish in a zoological setting. The reason for this apparent absence is unclear given the enormous numbers of ornamental fish kept and traded around the globe (Smith et al., 2017; Whittington and Chong, 2007).

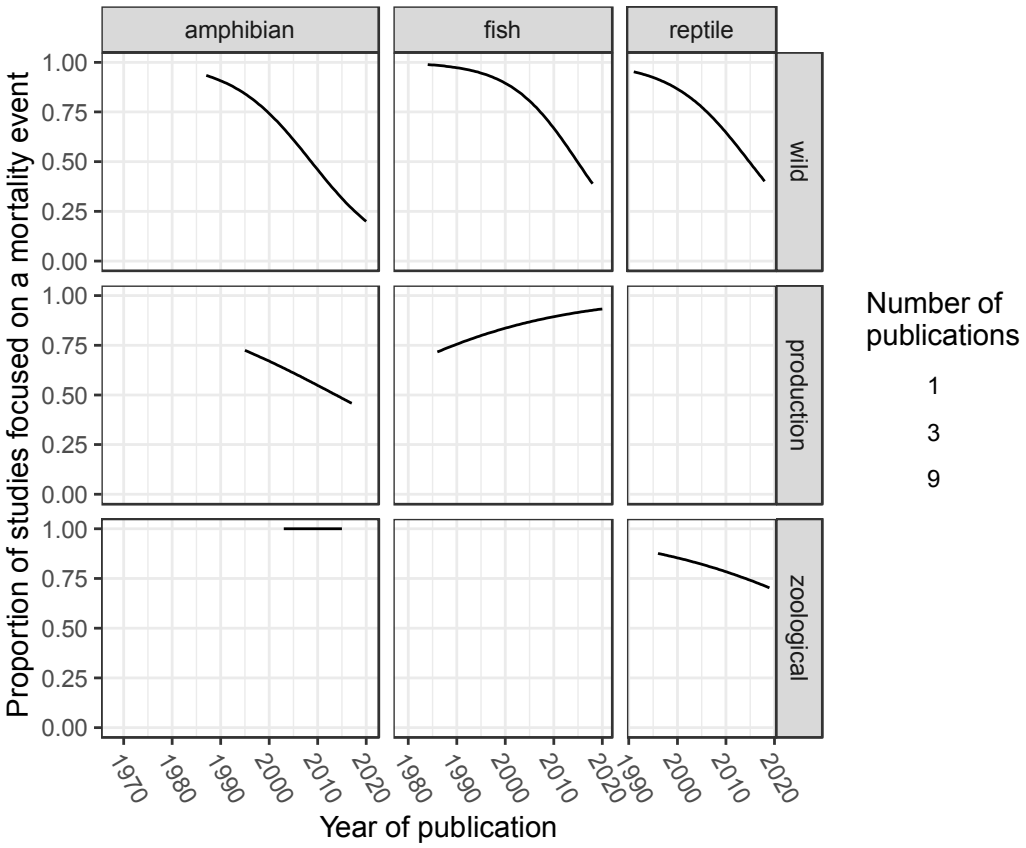

Figure 2: Proportion of publications in the GRRS that were initiated by host morbidity or mortality, as opposed to routine surveillance, when this information was provided. Black lines represent best-fit logistic regressions to illustrate trends.

Patterns in host taxonomy

We also see that most diversity at the genus level in the GRRS is found in amphibians, primarily anurans (n= 63), but fish (n=27) and reptile (n= 34) genera are also well represented (Table 1). This representation, however, is a fraction of the diversity within these classes. For instance, the 63 amphibian genera in the GRRS represents just 9.8% of the 646 currently recognized (AmphibiaWeb, 2020). Moreover, we are aware of no reports of ranaviruses in caecilians. Presumably this reflects limited search efforts more than a restricted host range. Similar to the numbers of reports, most host diversity in the GRRS comes from wild populations rather than production or zoological settings. This is perhaps not surprising in production settings, which involves relatively few host taxa overall, but zoos and private collections comprise a great deal of diversity and so the relative absence of reports in these settings suggests under-reporting. Moreover, this collective under-reporting should cause us pause before we use the diversity of hosts from which ranaviruses have been reported as a measure of host range more generally.

Table 1: The number of genera represented in the GRRS by taxonomic class, order, and family and type of population.

Class	Order	Family	Wild	Prod.	Zoo	Total
amphibian	Anura	Alytidae	1	0	1	2
amphibian	Anura	Batrachylidae	1	0	0	1
amphibian	Anura	Bombinatoridae	1	0	0	1
amphibian	Anura	Bufonidae	5	0	2	7
amphibian	Anura	Calyptocephalellidae	2	1	0	3
amphibian	Anura	Centrolenidae	3	0	0	3
amphibian	Anura	Craugastoridae	2	0	0	2
amphibian	Anura	Dendrobatidae	1	0	3	4
amphibian	Anura	Dicroglossidae	0	1	0	1
amphibian	Anura	Eleutherodactylidae	2	0	0	2
amphibian	Anura	Hylidae	7	0	1	8
amphibian	Anura	Leptodactylidae	2	0	0	2
amphibian	Anura	Limnodynastidae	1	0	0	1
amphibian	Anura	Microhylidae	2	0	0	2
amphibian	Anura	Pelobatidae	1	0	0	1
amphibian	Anura	Pelodryadidae	1	0	1	2
amphibian	Anura	Phyllomedusidae	1	0	0	1
amphibian	Anura	Pipidae	1	1	0	2
amphibian	Anura	Pyxicephalidae	0	0	1	1
amphibian	Anura	Ranidae	2	1	2	5
amphibian	Anura	Rhacophoridae	0	0	1	1
amphibian	Anura	Scaphiopodidae	2	0	0	2
amphibian	Anura	Telmatobiidae	1	0	0	1
amphibian	Urodela	Ambystomatidae	1	1	0	2
amphibian	Urodela	Cryptobranchidae	2	1	1	4
amphibian	Urodela	Plethodontidae	7	0	0	7
amphibian	Urodela	Salamandridae	8	0	0	8
fish	Acipenseriformes	Acipenseridae	0	1	0	1
fish	Actinopterygii	Anguillidae	0	1	0	1
fish	Actinopterygii	Gadidae	1	0	0	1
fish	Actinopterygii	Nemacheilidae	0	1	0	1
fish	Actinopterygii	Pomacentridae	0	1	0	1
fish	Actinopterygii	Scophthalmidae	0	1	0	1

fish	Centrarchiformes	Oplegnathidae	1	0	0	1
fish	Centrarchiformes	Percichthyidae	0	1	0	1
fish	Centrarchiformes	Terapontidae	0	1	0	1
fish	Cichliformes	Cichlidae	1	0	1	2
fish	Cypriniformes	Cobitidae	1	0	0	1
fish	Cypriniformes	Cyprinidae	1	1	0	2
fish	Gasterosteiformes	Gasterosteidae	1	0	0	1
fish	Gobiiformes	Butidae	1	1	0	2
fish	Perciformes	Centrarchidae	1	0	0	1
fish	Perciformes	Latidae	1	0	0	1
fish	Perciformes	Lutjanidae	1	0	0	1
fish	Perciformes	Percidae	1	1	0	2
fish	Perciformes	Serranidae	1	1	0	2
fish	Perciformes	Sparidae	1	0	0	1
fish	Salmoniformes	Salmonidae	0	1	0	1
fish	Scorpaeniformes	Cyclopteridae	1	1	0	2
fish	Siluriformes	Ictaluridae	2	0	0	2
fish	Siluriformes	Siluridae	1	1	0	2
reptile	Squamata	Agamidae	4	0	3	7
reptile	Squamata	Anguidae	1	0	1	2
reptile	Squamata	Chamaeleonidae	0	0	1	1
reptile	Squamata	Colubridae	1	0	0	1
reptile	Squamata	Dactyloidae	0	0	1	1
reptile	Squamata	Gekkonidae	0	0	1	1
reptile	Squamata	Iguanidae	0	0	1	1
reptile	Squamata	Lacertidae	1	0	0	1
reptile	Squamata	Phrynosomatidae	1	0	0	1
reptile	Squamata	Pythonidae	1	0	1	2
reptile	Squamata	Scincidae	0	0	1	1
reptile	Testudines	Chelydridae	1	0	0	1
reptile	Testudines	Emydidae	8	0	1	9
reptile	Testudines	Kinosternidae	2	0	0	2
reptile	Testudines	Testudinidae	1	0	3	4
reptile	Testudines	Trionychidae	2	0	0	2

Ranavirus geography

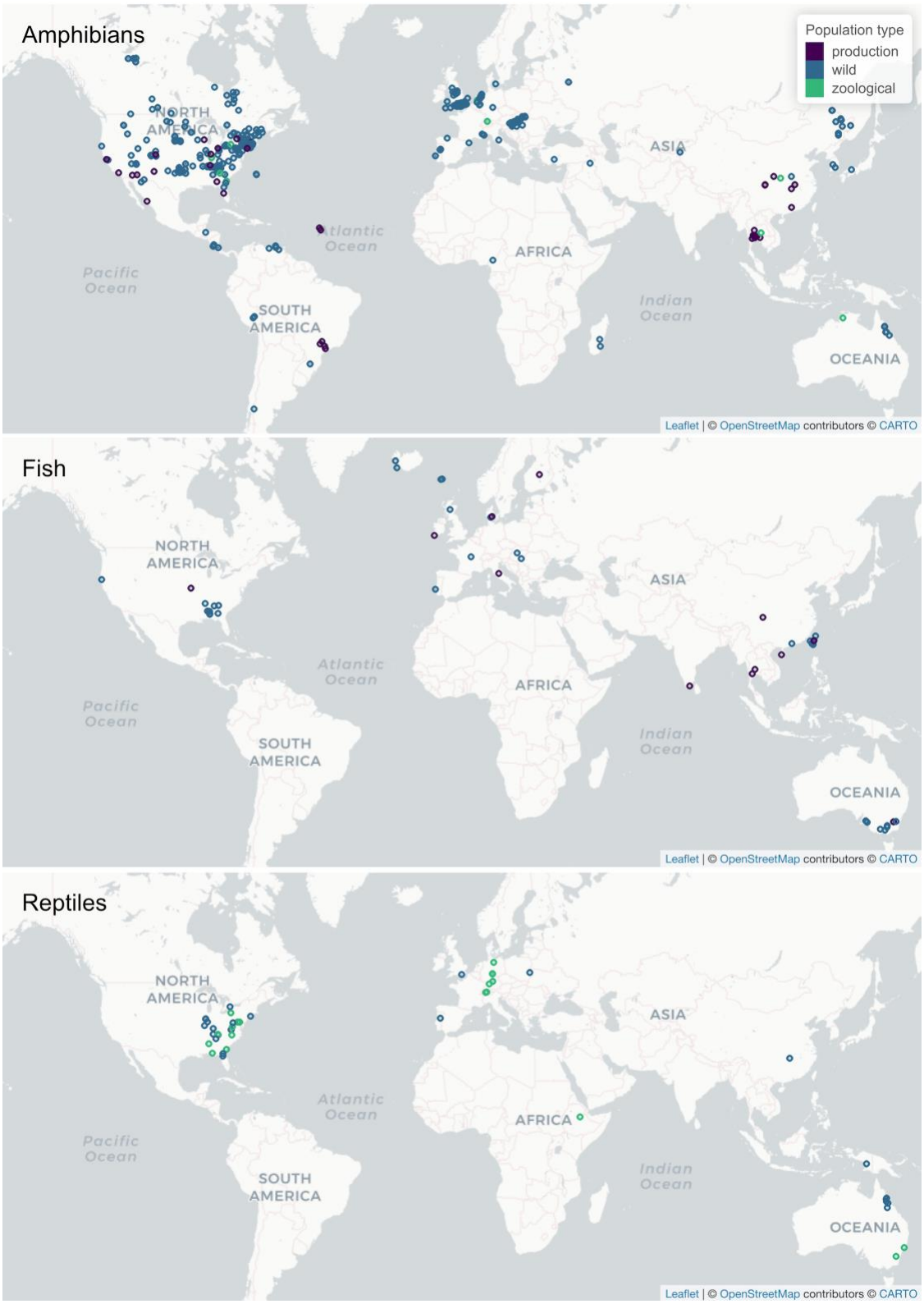

Figure 3: Map of ranavirus occurences in the GRRS from amphibians, fish, and reptiles according to the type of population, where available. Non-detections are included in the GRRS, but not shown in this figure.

The maps of ranavirus reports (Figure 3) illustrate a common pattern in disease detection: one finds infections where one looks. There is a clear bias towards reports in North America, Europe, and Southeast Asia. Reports from South America are sporadic and there are only three from Africa, including Madagascar. It is also worth noting that most reports of ranavirus are not from diversity hotspots (e.g., there are relatively few reports from amphibians in the tropics). Hence, one would expect that we have yet to discern the true geographic distribution (or host range) of ranaviruses. Most reports from production settings (e.g., ranaculture, aquaculture) are from Southeast Asia (i.e., China with 11, Thailand with four), but also from the United States (with reports) and Brazil (with an additional four).

Dominant modes of detection

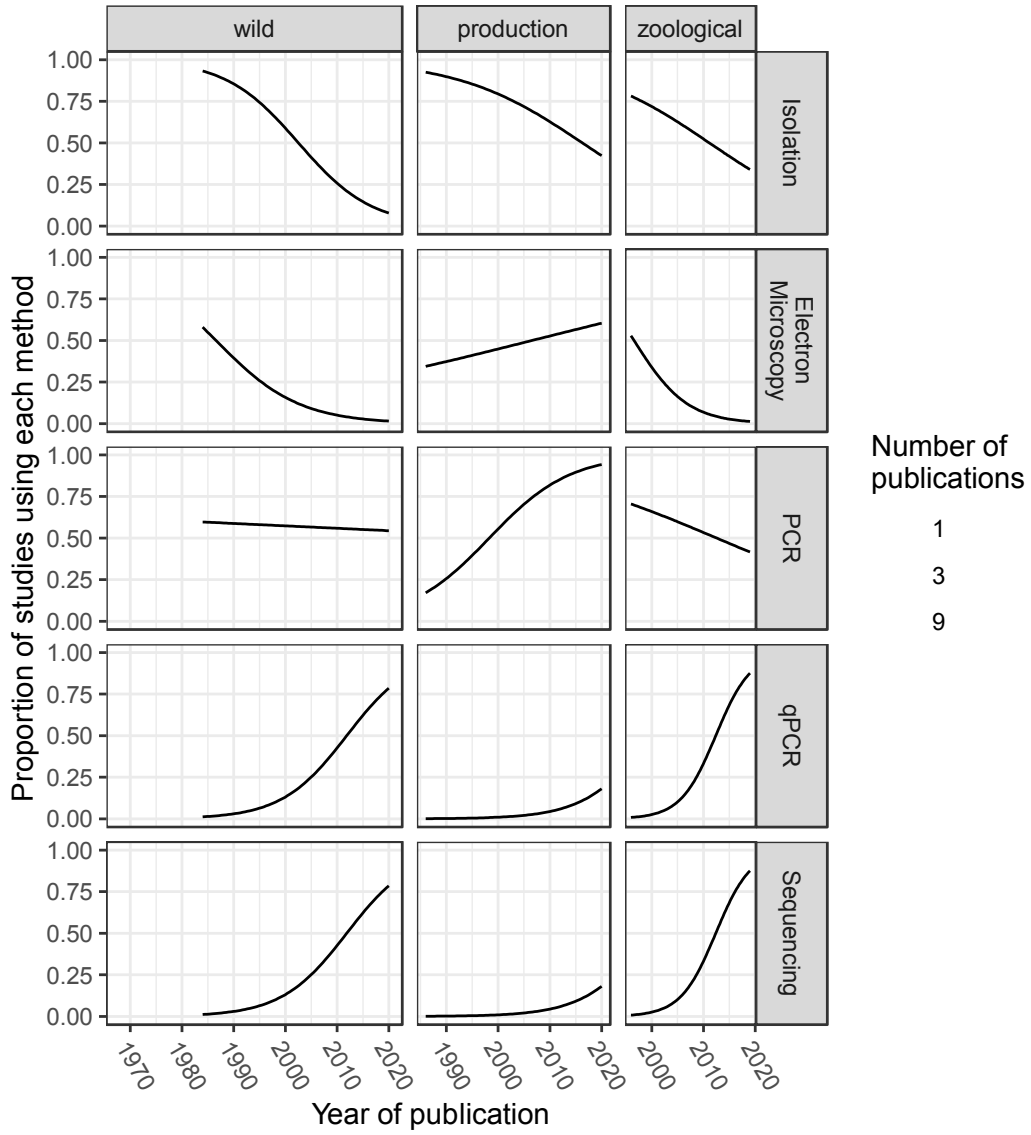

Figure 4: Methods of detecting ranavirus in publications in the GRRS over time according to population type. Note that a single publication might use several methods and so appear in several panels. Black lines represent best-fit logistic regressions to illustrate trends.

As the available diagnostic methods for detecting ranavirus have grown, their representation in the literature has changed (Figure 4). Virus isolation in culture has continued through at least the early 2010s, but has increasingly been replaced by molecular methods. Electron microscopy is increasingly rare except in production settings. Similarly, traditional PCR has largely been supplanted by quantitative, primarily Taqman real time PCR (qPCR). We suspect the broader adoption and relative ease of screening samples with (q)PCR methods is partially responsible for the increased routine testing of populations for ranaviruses and other pathogens (Fig. 2). Gene sequencing has also become increasingly common in certain contexts, presumably as prices have decreased, access

increased, and researchers have realized the biological significance of ranaviral species and genotypes. Much of this sequencing focuses on the major capsid protein gene and a few other genes, which may be useful in differentiating among ranavirus species (Tidona et al., 1998). However, with increasing evidence of inversions and recombination among strains (e.g., Claytor et al., 2017) we hope to see more and deeper sequencing to better characterize the ranaviruses being detected. We also hope that more researchers attempt to isolate ranaviruses. Virus isolates are the raw materials for subsequent experiments and viruses are known to evolve and attenuate with repeated passage in culture (Ebert, 1998). All that said, reports of ranavirus occurrence are interesting and useful even without these additional data. We encourage researchers to add their data to the GRRS, whatever their methods of detection, so that we can collectively describe ranavirus geography and host range.

Summary

Ranaviruses impact numerous ectothermic vertebrates of ecological and economic importance, as well as many of conservation concern (Brunner et al., 2015; Chinchar and Waltzek, 2014). Tracking their geographic distribution and host range is fundamental to understanding their basic biology, epidemiology, and evolution and for efforts to mitigate their impacts. Long-term datasets also permit us to understand the effects that emergence has on populations. The GRRS thus represents an important resource for researchers and multiple stakeholders.

Our efforts to summarize the trends in the GRRS offer a perspective on the state of knowledge about ranavirus distributions. We find that there is growing number of occurrences of ranaviruses and a growing diversity of hosts. We expect this reflects a growing interest and study of ranaviruses, along with broader interest in host conservation (e.g., amphibian declines more broadly). We suspect it also mirrors the growing ease with which researchers can screen samples for ranaviruses and other pathogens. Indeed, the proportion of studies stemming from routine surveillance as opposed to investigating morbidity or mortality has grown alongside the huge increases in reports overall. We expect that the increasing use of environmental DNA (eDNA) for pathogen detection in a variety of settings (e.g., Hall et al., 2016; Vilaça et al., 2019) will further increase our understanding of at least the geographic distribution of ranavirus nucleic acids. We plan to modify the GRRS to allow for eDNA samples, but encourage researchers to continue to screen hosts.

Our summary also makes clear that while records have increased dramatically, there still exist geographic and taxonomic biases. The vast majority of reports come from North America and thus North American species. Further sampling in South America, broader areas in Asia, and especially Africa will provide a much more complete picture of the geography of ranaviruses and their host ranges. Indeed, host ranges appears to be the most clearly biased aspect of our current sampling. One need only look to the severe under-representation of ranaviruses from fishes to appreciate the need for more surveillance in fishes. Additional sampling and genetic sequencing is also likely to add new viral species

that may help elucidate phylogenies and evolutionary relationships of these important, emerging viruses.

We hope that as the GRRS becomes more widely known, more researchers will add their records and use it as a research tool. We have attempted to create a useful, open, free tool for ranavirus researchers, but in the end the GRRS will be as successful as the community makes it.

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References

AmphibiaWeb, 2020. University of California, Berkeley, CA, USA [WWW Document]. URL https://amphibiaweb.org/

Blaustein, A., Urbina, J., Snyder, P., Reynolds, E., Dang, T., Hoverman, J., Han, B., Olson, D., Searle, C., Hambalek, N., 2018. Effects of emerging infectious diseases on amphibians: A review of experimental studies. Diversity 10, 81.

Brunner, J., Storfer, A., Gray, M., Hoverman, J., 2015. Ranavirus ecology and evolution: From epidemiology to extinction, in: Gray, M.J., Chinchar, V.G. (Eds.), Ranaviruses: Lethal Pathogens of Ecothermic Vertebrates. Springer International Publishing, Cham, Switzerland, pp. 71–104.

Chinchar, V.G., Waltzek, T.B., 2014. Ranaviruses: Not just for frogs. PLoS Pathogens 10, e1003850.

Claytor, S.C., Subramaniam, K., Landrau-Giovannetti, N., Chinchar, V.G., Gray, M.J., Miller, D.L., Mavian, C., Salemi, M., Wisely, S., Waltzek, T.B., 2017. Ranavirus phylogenomics: Signatures of recombination and inversions among bullfrog ranaculture isolates. Virology 511, 330–343.

Daszak, P., Berger, L., Cunningham, A.A., Hyatt, A.D., Green, D.E., Speare, R., 1999. Emerging infectious diseases and amphibian population declines. Emerg Infect Dis 5, 735–748.

Duffus, A.L.J., Waltzek, T.B., Stöhr, A.C., Allender, M.C., Gotesman, M., Whittington, R.J., Hick, P., Hines, M.K., Marschang, R.E., 2015. Distribution and host range of ranaviruses, in: Gray, M.J., Chinchar, V.G. (Eds.), Ranaviruses: Lethal Pathogens of Ecothermic Vertebrates. Springer International Publishing, Cham, Switzerland, pp. 9–57.

Duffus, A., Olson, D., 2011. The establishment of a Global Ranavirus Reporting System. FrogLog 96, 37.

Ebert, D., 1998. Experimental evolution of parasites. Science 282, 1432–1435.

Granoff, A., Came, P.E., Rafferty, K.A., 1965. The isolation and properties of viruses from *rana pipiens*: Their possible relationship to the renal adenocarcinoma of the leopard frog. Annals of the New York Academy of Science 126, 237–255.

Hall, E., Crespi, E., Goldberg, C., Brunner, J., 2016. Evaluating environmental DNA-based quantification of ranavirus infection in wood frog populations. Mol Ecol Resour 16, 423–433.

ICTV, "International Commitee on the Taxonomy of Viruses", 2020. The ICTV report on virus classification and taxon nomenclature, *Iridoviridae, Ranavirus*. [WWW Document]. URL https://talk.ictvonline.org/ictv-reports/ictv_online_report/dsdna-viruses/w/iridoviridae/616/genus-ranavirus

OIE, "World Organization for Animal Health", 2020. WAHIS portal: Animal Health Data [WWW Document]. URL https://www.oie.int/en/animal-health-in-the-world/wahis-portal-animal-health-data/

Rafferty, K.J., 1965. The cultivation of inclusion-associated viruses from Lucke tumor frogs. Ann N Y Acad Sci 126, 3–21.

Schloegel, L.M., Daszak, P., Cunningham, A.A., Speare, R., Hill, B., 2010. Two amphibian diseases, chytridiomycosis and ranaviral disease, are now globally notifiable to the World Organization for Animal Health (OIE): An assessment. Dis Aquat Organ 92, 101–108.

Smith, K., Zambrana-Torrelio, C., White, A., Asmussen, M., Machalaba, C., Kennedy, S., Lopez, K., Wolf, T., Daszak, P., Travis, D., Karesh, W., 2017. Summarizing US wildlife trade with an eye toward assessing the risk of infectious disease introduction. Ecohealth 14, 29–39.

Stagg, H., Guðmundsdóttir, S., Vendramin, N., Ruane, N., Sigurðardóttir, H., Christiansen, D., Cuenca, A., Petersen, P., Munro, E., Popov, V., Subramaniam, K., Imnoi, K., Waltzek, T., Olesen, N., 2020. Characterization of ranaviruses isolated from lumpfish *Cyclopterus lumpus* L. In the North Atlantic area: Proposal for a new ranavirus species (European North Atlantic Ranavirus). J Gen Virol 101, 198–207.

Stöhr, A., Fleck, J., Mutschmann, F., Marschang, R., 2013. Ranavirus infection in a group of wild-caught Lake Urmia newts *Neurergus crocatus* imported from Iraq into Germany. Dis Aquat Org 103, 185–189.

Stöhr, A., Hoffmann, A., Papp, T., Robert, N., Pruvost, N., Reyer, H., Marschang, R., 2013. Long-term study of an infection with ranaviruses in a group of edible frogs (*Pelophylax kl. Esculentus*) and partial characterization of two viruses based on four genomic regions. Vet J 197, 238–244.

Tidona, C.A., Schnitzler, P., Kehm, R., Darai, G., 1998. Is the major capsid protein of iridoviruses a suitable target for the study of viral evolution. Virus genes 16, 59–66.

Vilaça, S.T., Grant, S.A., Beaty, L., Brunetti, C.R., Congram, M., Murray, D.L., Wilson, C.C., Kyle, C.J., 2019. Detection of spatiotemporal variation in ranavirus distribution using eDNA. Environmental DNA.

Whittington, R., Chong, R., 2007. Global trade in ornamental fish from an Australian perspective: The case for revised import risk analysis and management strategies. Preventive Veterinary Medicine 81, 92–116.