



Invited review

Novel viruses in birds: Flying through the roof or is a cage needed?

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ABSTRACT

Emerging viral diseases continue to have a major global impact on human beings and animals. To be able to take adequate measures in case of an outbreak of an emerging disease, rapid detection of the causative agent is a crucial first step. In this review, various aspects of virus discovery are discussed, with a special focus on recently discovered viruses in birds. Novel viruses with a potential major impact have been discovered in domestic and wild bird species in recent years using various virus discovery methods. Only a few studies report the detection of novel viruses in endangered bird species, although increased knowledge about viruses circulating in these species is important. Additional studies focusing on the exact role of a novel virus in disease and on the impact of a novel virus on bird populations are often lacking. Intensive collaboration between different disciplines is needed to obtain useful information about the role of these novel viruses.

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Introduction

Emerging viruses continue to cause major outbreaks of disease and mortality among human beings and animals worldwide. A recent example of such an outbreak among birds is the highly pathogenic avian influenza virus (HPAIV) A (H5N8) in Europe which started in autumn 2016 (Pohlmann et al., 2017). While a HPAIV A (H5N8) virus had already spread in autumn and winter of 2014–2015 from Asia to North-America and Europe, a different variant emerged in 2016–2017, causing high mortalities among both wild birds and domestic poultry (Global Consortium for H5N8 and Related Influenza Viruses, 2016; Kleyheeg et al., 2017; More et al., 2017; Pohlmann et al., 2017).

There are several other viruses that have caused major outbreaks among domestic or wild birds recently, or are continuously circulating among birds worldwide (de Wit et al., 2011; Pello and Olsen, 2013; Chan et al., 2015). An example is the widespread outbreak of Usutu virus, a mosquito-borne flavivirus in 2016 in Europe, mainly among common blackbirds (*Turdus merula*) (Rijks et al., 2016; Cadar et al., 2017; Garigliany et al., 2017). Another example is duck tembusuvirus (DTMUV), a member of the *Flaviviridae* (Liu et al., 2013). The first outbreaks of this novel virus started in spring 2010 on duck farms in southeast China. Infection resulted in a decline in feed uptake and a major drop in egg production in laying ducks. DTMUV was quickly isolated and genetically characterised from tissue samples collected from

affected ducks, while the disease could be reproduced by experimental infection of laying ducks (Cao et al., 2011; Su et al., 2011; Yan et al., 2011; Liu et al., 2013). Viruses closely related to DTMUV have also been found in ducks in various other countries in Asia, and in various other bird species, including the house sparrow (*Passer domesticus*) (Liu et al., 2013; Tang et al., 2013; Homonnay et al., 2014; Thontiravong et al., 2015).

There has been an enormous increase in the number of live domestic birds; the Food and Agriculture Organization (FAO) of the United Nations estimated that there were 3,906,690,000 live chickens worldwide in 1962, 13,518,655,000 in 1996 and 21,409,683,000 in 2014.¹ There has also been an increase in the number of endangered (EN) and critically endangered (CE) species of birds; out of a total of 11,121 avian species, the International Union for Conservation of Nature (IUCN) recorded 403 EN and CE species in 1996, and 773 EN and CE species in 2016.² This indicates that, from both an economical and wild bird conservation perspective, it is important to gain insights into currently unknown viruses that circulate among wild and domestic birds. A relatively high proportion of species of the orders *Accipitriformes* (11%; diurnal birds of prey), *Galliformes* (10%; heavy-bodied ground-feeding birds), *Gruiformes* (11%; wading and terrestrial birds), *Procellariiformes* (23%; seabirds) and *Sphenisciformes* (14%; penguins) are currently (critically) endangered and discovery of novel

¹ See: Food and Agriculture Organization (FAO) of the United Nations <http://faostat3.fao.org/download/T/TA/E> (accessed 1 January 2018).

² See: The IUCN Red List of Threatened Species. Version 2016-3 <http://www.iucnredlist.org> (accessed 1 January 2018).

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viruses in clinical cases of these bird species may be of value in species protection.

Viral metagenomics, the use of next generation sequencing (NGS) for unbiased metagenomic analyses of viral communities, is a rapid and accurate method for detecting novel viral sequences in animals with and without disease (Delwart, 2012; Mokili et al., 2012; Belák et al., 2013). The rapid availability of novel sequencing techniques and the steady lowering of the costs of viral metagenomics, means that it is becoming easier to gain insights into viruses that circulate among both domestic birds and birds.

The aim of this review is provide an overview of recent developments in the field of virus discovery in wild and domestic birds, to bring these findings into perspective, and to highlight challenges and pitfalls for future research in the field of viral metagenomics of wild and domestic birds.

Virus discovery: Aims, sample selection, collection and methods

The aim of virus discovery can be: (1) to detect novel viruses in samples collected from animals with disease of unknown origin; (2) to detect all viruses, including currently unknown viruses, in a host in a certain region that might be harmful for other hosts, including potential zoonotic agents; (3) to detect novel viruses in a sample to increase the knowledge about viral diversity (in a special host or region); or (4) to provide a baseline level of viruses present in healthy animals in case future outbreaks occur.

To discover a novel virus that might be related to a disease or mortality outbreak among animals, a step-by-step approach could be followed from clinical or post-mortem examination to elucidation of the pathogenicity and epidemiology of the novel virus (Fig. 1). This step-by-step approach starts with a complete

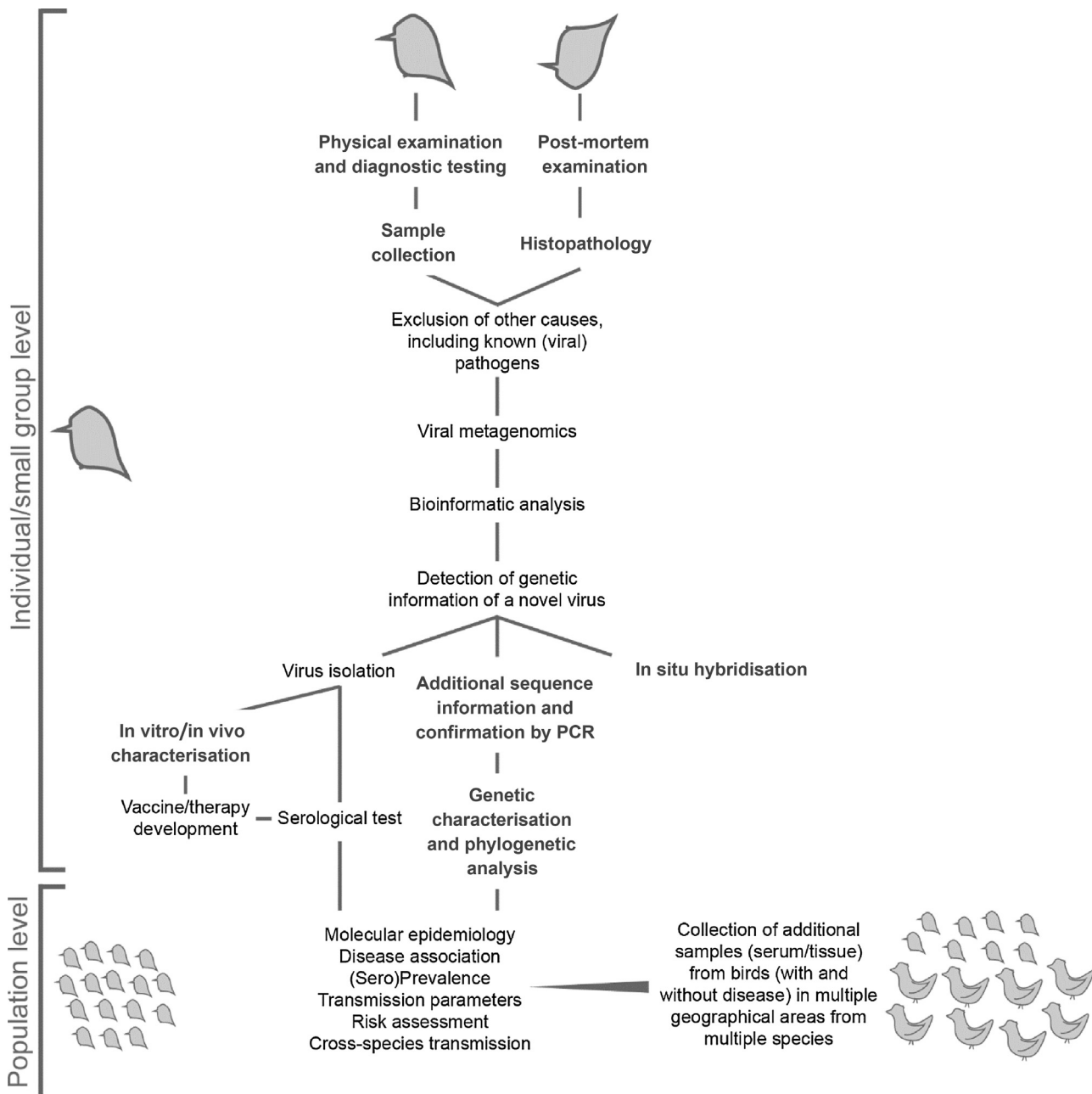


Fig. 1. Step-by-step virus discovery approach from the individual bird or a small group of birds to a population of birds.

and well described clinical case series of (preferably multiple) live animals or thorough histopathological examinations of animals that have died due to disease of unknown origin. Information that could indicate a viral aetiology rather than other causes are, for example, the presence of viral inclusion bodies, histopathological evidence of inflammation without visible or culturable bacteria or parasites, epidemiological clustering of cases (although differentiation from intoxication is needed) and epidemiological evidence for apparent transmission from one animal to another.

If the information obtained suggests a viral disease, various standard laboratory tests, such as antigen ELISA, conventional PCR (with specific primer sets and, subsequently, degenerate primer sets to detect broader virus families) and quantitative PCR (qPCR), can be performed to test for the presence of known viruses. When no pathogens can be detected with these tests, viral metagenomics can be performed to provide an overview of viruses (known and unknown) that are present. However, since this technique is highly sensitive to contamination, great care must be taken with sample collection. Furthermore, many viruses are only commensals and confirmation by other independent methods, and extensive additional studies, are necessary to claim a link between the novel virus and the disease (Bukowska-Ośko et al., 2016).

The availability of NGS technologies has greatly improved the possibility of detecting novel viral sequences, although cell culture, electron microscopy and conventional PCR (with degenerate primers) are still relevant and frequently used to detect (novel) viruses in various animal species. In recent years, various improvements in sequencing techniques have been developed. This has resulted in an enormous increase in the number of reads that can be obtained from a single sample. However, adequate bioinformatics analysis has become increasingly crucial to obtain the most valuable output from the raw data (Kapgata et al., 2015; Höper et al., 2016; Kumar et al., 2017).

After discovery of a previously unknown viral sequence, often the complex and time-consuming part of obtaining the complete or near complete genome starts. Obtaining a (near) complete genome is of great interest for several reasons: (1) to study the genome organisation of that particular virus; (2) to allow recognition of the viral sequence by BLAST³ for future virus discovery experiments; (3) to study the molecular epidemiology of that virus if additional samples are available; (4) to elucidate the impact of certain mutations in the future that might affect the virulence of the virus; and (5) to provide an indication of the proteins it possesses, their potential pathogenic effects and if any current drugs or vaccines might work. The deduced amino acid sequence also allows the study of the expression of protein sequences for the development of protein/antibody-based diagnostics.

Approaches that could be used to obtain the full sequences of relatively large genomes generally include a combination of various assembly approaches using NGS data and standard PCR using newly developed primers and sequencing (Smits et al., 2014; Vázquez-Castellanos et al., 2014; Orton et al., 2016). Obtaining as much genome information as possible is also very useful to elucidate whether the novel virus is a novel variant or strain, species, genus or even family. The International Committee on Taxonomy of Viruses (ICTV) has agreed that viruses known from metagenomics data can, and should be, incorporated in the official classification scheme (Simmonds et al., 2017).⁴

Virus discovery: What's next?

The initial discovery of a novel virus or virus variant is only a first step and requires additional studies to elucidate the origin of the virus, whether the virus has any role in disease in the same or other hosts, the possibility of variants with enhanced pathogenicity and the impact of the virus on the population. Furthermore, if multiple viruses are detected in a single sample, the role of each of these viruses in the observed disease should be evaluated.

Disease causation

To demonstrate a role of a novel virus in a certain disease in an animal, a first step could be to detect viral proteins or genetic material in tissues with associated lesions by *in situ* hybridisation (ISH) or immunohistochemistry (IHC). While detection of a virus by PCR or viral metagenomics in homogenised tissues provides an indication that the virus is indeed present in the tissue, it does not exclude the possibility that the virus is present in blood circulating within the tissues. ISH can be used to detect viral RNA or DNA directly in formalin-fixed tissues, without the need for production of monoclonal antibodies against viral proteins.

To fulfil Koch's postulates, the role of a virus in acute disease can be demonstrated if the virus can be isolated in cells or embryonated eggs and subsequently inoculated in the host of the same age and breed or species from which the virus was isolated, reproducing the same disease. However, this is often impossible if no viral isolate can be obtained or if the host in which the virus was detected was a wild animal, also taking ethical considerations into account. Furthermore, many diseases in which viruses are involved are often multifactorial, which complicates efforts to study the role of a virus in a certain disease in an artificial animal model, such as chickens or chicken embryo models for avian viruses (Hess, 2017). Metagenomic Koch's postulates have been proposed recently (Mokili et al., 2012), but in many cases it will still be difficult to demonstrate proof of causality in natural hosts in wild animal populations.

Impact on populations

Virus discovery often starts with a relatively small number of samples, especially when samples are collected from wild animals. However, to understand the impact of a novel virus on a population, additional samples are necessary from both healthy and diseased birds in multiple geographical areas at multiple time points to study the prevalence, to estimate transmission parameters, to perform disease association studies and to undertake risk assessments. In addition, it could be of interest to test samples from other animal species that live in close contact to study possible cross-species transmission or to determine the origin of the novel virus. However, for acute viral diseases, the rates of detection of the viral pathogens by PCR are most likely to be low and high numbers of samples are needed. Based on the outcome of these studies, it can be decided whether it could be useful, either from an economical, public health or wildlife conservation perspective, to take measures to prevent spread of the virus and to develop vaccines.

Overview of recently discovered viruses in birds

Numerous novel viruses and virus variants have been discovered in birds in recent years. Chan et al. (2015) provided an overview of examples of novel avian viruses published from 2012 to 2014. To extend this overview to 2017, a literature search on

³ See: <https://blast.ncbi.nlm.nih.gov/Blast.cgi> (accessed 1 January 2018).

⁴ See: International Committee on Taxonomy of Viruses (ICTV). Virus Taxon. 2016 Release. <https://talk.ictvonline.org/taxonomy/> (accessed 1 January 2018).

Table 1
Selection of novel viruses recently discovered in captive (cage, aviary and ornamental) birds.

Virus family	Virus name	Host (Latin name)	Disease	Additional studies		Reference
				Pathology	Epidemiology	
<i>Adenoviridae</i>	Poicephalus adenovirus	Red-bellied parrot (<i>Poicephalus rufiventris</i>)	Acute necrotising hepatitis	ND	ND	Das et al., 2017
<i>Adenoviridae</i>	Psittacine adenovirus HKU1	Mealy parrot (<i>Amazona farinosa</i>)	Co-infection with <i>Chlamydia psittaci</i>	Histopathology and IHC	Small prevalence study	To et al., 2014
<i>Bornaviridae</i>	Parrot bornavirus 2014-A	Blue-and-yellow macaw (<i>Ara ararauna</i>)	Proventricular dilatation disease	Histopathology	ND	Marton et al., 2015
<i>Bornaviridae</i>	Parrot bornavirus 5	Palm cockatoo (<i>Probosciger aterrimus</i>)	Proventricular dilatation disease	ND	ND	Guo and Tizard, 2015
<i>Bornaviridae</i>	Parrot bornavirus 8 USP/NP-33/BRAZIL/2012 USP/NP-34/BRAZIL/2012 USP/NP-42/BRAZIL/2012 USP/NP-47/BRAZIL/2012 USP/NP-48/BRAZIL/2012 USP/NP-49/BRAZIL/2012	Blue-fronted amazon (<i>Amazona aestiva</i>)	Proventricular dilatation disease	ND	Small prevalence study	Philadelpho et al., 2014
<i>Bornaviridae</i>	Parrot bornavirus 8 USP/NP-63/BRAZIL/2012	White cockatoo (<i>Cacatua alba</i>)	Proventricular dilatation disease	ND	Small prevalence study	Philadelpho et al., 2014
<i>Bornaviridae</i>	Parrot bornavirus 8 USP/NP-93/BRAZIL/2012	Golden conure (<i>Guaruba guarouba</i>)	Proventricular dilatation disease	ND	Small prevalence study	Philadelpho et al., 2014
<i>Herpesviridae</i>	Phoenicopterid herpesvirus 1	Chilean flamingo (<i>Phoenicopterus chilensis</i>)	Pneumonia, hepatopathy, anaemia	Histopathology, EM	ND	Coverdill et al., 2016

ND, no data; IHC, immunohistochemistry; EM, electron microscopy.

PubMed⁵ was performed using the keywords ‘virus’ and ‘bird’ to identify manuscripts that explicitly focus on novel viruses; based on title and abstract; and published from October 2014 to March 2017. An overview of the manuscripts from which the data were analysed during this literature search is listed in Appendix: Supplementary Table S1. Novel viruses belonging to the families of *Adenoviridae*; *Astroviridae*; *Bornaviridae*; *Bunyaviridae*; *Circoviridae*; *Coronaviridae*; *Flaviviridae*; *Hepadnaviridae*; *Hepeviridae*; *Herpesviridae*; *Orthomyxoviridae*; *Papillomaviridae*; *Paramyxoviridae*; *Parvoviridae*; *Picornaviridae*; *Picornaviridae*; *Polyomaviridae*; *Poxviridae*; *Reoviridae*; *Retroviridae* and *Rotaviridae* were discovered and characterised during this period. Novel viruses were described mainly from wild birds; but novel viruses also were detected in various species of captive birds and poultry. Amongst wild birds; novel viruses were discovered in four species listed as endangered; namely the African penguin (*Spheniscus demersus*); rowi kiwi (*Apteryx rowi*); vinaceous-breasted amazon (*Amazona vinacea*) and white cockatoo (*Cacatua alba*); and two species listed as vulnerable; namely the golden conure (*Guaruba guarouba*) and the velvet scoter (*Melanitta fusca*); while no novel viruses were discovered in species that were critically endangered.

Novel viruses in cage, aviary and ornamental birds

In cage, aviary and ornamental birds, novel members of the *Adenoviridae*, *Bornaviridae*, *Herpesviridae* and *Polyomaviridae* families were discovered (Table 1; see Appendix: Supplementary Table S1); for all of these viruses, there was evidence for involvement in the observed disease based on the published data and current knowledge about closely related viruses and/or hosts.

A novel aviadenovirus was discovered in red-bellied parrots (*Poicephalus rufiventris*) in Australia with histological evidence of acute necrotising hepatitis (Das et al., 2017). Another novel adenovirus was detected in mealy parrots (*Amazona farinosa*) co-

infected with *Chlamydia psittaci* during the investigation of a human psittacosis outbreak in Hong Kong (To et al., 2014). This virus was not found in healthy parrots unrelated to the outbreak and the adenovirus viral load was correlated with the *C. psittaci* load in the lungs. Novel bornaviruses have been detected in several bird species with proventricular dilatation disease (Table 1) (Philadelpho et al., 2014; Guo and Tizard, 2015; Komorizono et al., 2016). A novel alphaherpesvirus was discovered in a sample of liver collected from a juvenile Chilean flamingo, held in captivity in California, USA, with fatal pneumonia, hepatopathy and anaemia; this novel alphaherpesvirus was most closely related to gaviid herpesvirus 1 (Coverdill et al., 2016).

Novel viruses in wild birds

A wide diversity of novel viruses has been found in wild birds, with novel members of the families *Astroviridae*, *Bornaviridae*, *Bunyaviridae*, *Circoviridae*, *Coronaviridae*, *Flaviviridae*, *Hepeviridae*, *Herpesviridae*, *Orthomyxoviridae*, *Papillomaviridae*, *Paramyxoviridae*, *Picornaviridae*, *Polyomaviridae*, *Poxviridae*, *Reoviridae*, *Retroviridae* and *Rotaviridae* being discovered in recent years (Table 2; see Appendix: Supplementary Table S1).

An important finding was the discovery of Wellfleet Bay virus, a novel orthomyxovirus, the potential causative agent of cyclical mortality events since 1998 in common eiders (*Somateria mollissima dresseri*) along the coasts of Cape Cod, Massachusetts, USA (Allison et al., 2015). Although multiple factors most likely have contributed to these mortality events, which involve thousands of birds, the detection of this novel virus in several moribund animals and the detection of Wellfleet Bay virus antigen in post-mortem specimens with histological lesions indicates that this virus may play a role in the mortality events. There is serological evidence that Wellfleet Bay virus emerged among common eiders in Massachusetts in 2006 (Ballard et al., 2017).

A novel picornavirus (poecivirus) was discovered in black-capped chickadees (*Poecile atricapillus*), in Alaska, with avian keratin disorder, which is characterised by a debilitating

⁵ See: <https://www.ncbi.nlm.nih.gov/pubmed> (accessed 1 March 2017).

Table 2
Selection of novel viruses recently discovered in wild birds.

Virus family	Virus name	Host (<i>Latin name</i>)	Disease	Additional studies		Reference
				Pathology	Epidemiology	
<i>Circoviridae</i>	Gyrovirus 8	Northern fulmar (<i>Fulmarus glacialis</i>)	Head tilt, ataxia	Histopathology	Small prevalence study	Li et al., 2015
<i>Circoviridae</i>	Rowi kiwi Circovirus-like virus	Rowi kiwi (<i>Apteryx rowi</i>)	Dermatitis	ND	ND	White et al., 2016
<i>Flaviviridae</i>	USU-BE-Lincent/2016	Blackbird (<i>Turdus merula</i>)	Found dead	Histopathology and IHC	ND	Garigliany et al., 2017
<i>Flaviviridae</i>	Usutu-BONN	Blackbird (<i>Turdus merula</i>)	Found dead	ND	ND	Cadar et al., 2015
<i>Herpesviridae</i>	African penguin herpesvirus-like virus	African penguin (<i>Spheniscus demersus</i>)	Pneumonia, emaciation	Histopathology	ND	Parsons et al., 2015
<i>Orthomyxoviridae</i>	Wellfleet Bay virus	Common eider (<i>Somateria mollissima</i>)	Mass mortality, variety of clinical signs	Histopathology and IHC	Outbreak investigation	Allison et al., 2015
<i>Papillomaviridae</i>	<i>Fulmarus glacialis</i> papillomavirus 1	Northern fulmar (<i>Fulmarus glacialis</i>)	Emaciation, ulcerative dermatitis, pedunculated masses	Histopathology	ND	Gaynor et al., 2015
<i>Picornaviridae</i>	Poecivirus	Black-capped chickadee (<i>Poecile atricapillus</i>)	Avian keratin disorder	Histopathology, tissue tropism	Disease association study	Zylberberg et al., 2016
<i>Poxviridae</i>	Avipoxvirus ID8501092	Stone-curlew (<i>Burhinus oedicephalus</i>)	Wart-like lesions and nodules	Histopathology	ND	Lecis et al., 2017
<i>Reoviridae</i>	Magpie reovirus	Magpie (<i>Pica pica</i>)	Moribund, hepatic and splenic necrosis	Histopathology, EM, ISH	ND	Lawson et al., 2015

ND, no data available; IHC, immunohistochemistry; ISH, in situ hybridisation, EM, electron microscopy.

overgrowth of the avian beak (Zylberberg et al., 2016). This disorder is an increasingly common disease of various species of wild birds in widespread geographical locations. In a disease association study among black-capped chickadees, birds with avian keratin disorder were more frequently infected with this novel virus than healthy controls. In addition, the virus was also detected in two other bird species with avian keratin disorder.

A novel poxvirus was detected by PCR in large wart-like lesions and nodules on the legs and toes of a wild stone curlew (*Burhinus oedicephalus*) from Sardinia, Italy (Lecis et al., 2017). In a northern fulmar (*Fulmarus glacialis*), stranded on the Californian coast, with severe emaciation, ulcerative dermatitis and pedunculated masses on the foot, a novel papillomavirus was identified in the papillomatous masses by electron microscopy and PCR (Gaynor et al., 2015). This papillomavirus belongs to a putative novel genus and was present in a lesion not previously associated with papillomaviruses, possibly demonstrating a novel mechanism of productive viral papillomavirus infection.

Infection with a novel reovirus was associated with hepatic and splenic necrosis in a magpie (*Pica pica*) from England, UK (Lawson et al., 2015).

In addition to the discovery of these viruses in wild birds, in which there was clear evidence for a role in the observed disease or mortality, other novel viruses were discovered for which a role in disease is unclear. A novel gyrovirus was detected in the spleen and uropygial gland of a northern fulmar, stranded on the Californian coast, with head tilt and ataxia (Li et al., 2015). This gyrovirus is the first non-chicken gyrovirus discovered, but the exact role of the novel virus in the disease could not be elucidated, especially since the virus was not detected in samples collected from other fulmars with similar clinical signs or pathology (Li et al., 2015).

A novel circovirus-like virus was discovered in the faeces of rowi kiwis in New Zealand, but the pathogenicity of this virus is unknown (White et al., 2016). A herpesvirus-like virus was detected in juvenile African penguins with respiratory disease at a rehabilitation centre in South Africa by histopathology and electron microscopy, but PCR was negative and the role of the putative virus in the disease could not be determined (Parsons et al., 2015).

Novel viruses in pigeons

A novel alphaherpesvirus was isolated from the liver and spleen of pigeons (*Columba livia domestica*) during an outbreak of increased mortality among a flock used for meat production in China (Zhang et al., 2015). Intraperitoneal inoculation of young pigeons with the virus resulted in systemic infection, with multifocal necrosis in the liver and spleen, although none of the inoculated pigeons died. During an outbreak of young pigeon disease syndrome (YPDS), a novel adenovirus was discovered by electron microscopy, followed by whole genome sequencing, in faeces collected from diseased pigeons in Germany (Teske et al., 2017). However, a disease association study revealed that there was no indication of a correlation between YPDS and the presence of this novel adenovirus (Table 3; see Appendix: Supplementary Table S1). A novel circovirus was detected during an outbreak of diarrhoea of an unknown cause among racing pigeons in Japan (Yamamoto et al., 2015). Although various other possible causes of diarrhoea in these pigeons were excluded, the role of this novel circovirus in the disease remains unclear.

Novel viruses in chickens

A number of novel viruses have been reported recently in chickens (Table 3; see Appendix: Supplementary Table S1). Infection with a novel chicken astrovirus was associated with increased mortality of embryos and chicks, and weakness and white plumage ('white chicks' condition), in hatched chicks in Poland in 2013, supported by metagenomics and experimental inoculation (Sajewicz-Krukowska et al., 2016; Sajewicz-Krukowska and Domanska-Blicharz, 2016).

Three novel picornaviruses have been described in chickens recently, but their role in disease is unclear. In a single sample collected from a chicken with diarrhoea from a backyard farm in Hungary, eight different picornaviruses could be detected, including a novel virus, chicken phacovirus 1; a subsequent prevalence study using samples collected from different poultry flocks in the USA indicated that infection with this virus is widespread (Boros et al., 2016). Another picornavirus, a scicivirus, was

Table 3
Selection of novel viruses recently discovered in domestic birds.

Virus family	Virus name	Host (Latin name)	Disease	Additional studies		Reference
				Pathology	Epidemiology	
<i>Adenoviridae</i>	Pigeon adenovirus 2	Pigeon (<i>Columba livia domestica</i>)	Young pigeon disease syndrome	ND	Disease causation study; no causative role observed	Teske et al., 2017
<i>Astroviridae</i>	Chicken astrovirus PL/G059/2014	Chicken (<i>Gallus domesticus</i>)	'White chicks' condition	ND	ND	Sajewicz-Krukowska and Domanska-Blicharz, 2016
<i>Bunyaviridae</i>	Batai virus ZJ2014	Muscovy duck (<i>Cairina moschata</i>)	Decreased egg production	In vitro/in vivo	ND	Zhang et al., 2017
<i>Circoviridae</i>	Pigeon circovirus/Japan/2/2010	Pigeon (<i>Columba livia domestica</i>)	Diarrhoea	Histopathology, no significant lesions	ND	Yamamoto et al., 2015
<i>Flaviviridae</i>	Duck tembusuvirus-AH2011	Domestic duck (<i>Anas platyrhynchos domesticus</i>)	Duck haemorrhagic oophoritis	Gross pathology	ND	Wang et al., 2015
<i>Flaviviridae</i>	Tembusu virus D1921/1/3/MY and D1977/1/MY	Domestic duck (<i>Anas platyrhynchos domesticus</i>)	Neurological signs, death due to starvation	Histopathology; in vivo pathogenicity	Outbreak investigation	Homonnay et al., 2014
<i>Flaviviridae</i>	Tembusuvirus CQW1	Domestic duck (<i>Anas platyrhynchos domesticus</i>)	Loss of appetite, neurological signs, sudden death	Histopathology; in vivo pathogenicity	ND	Zhu et al., 2015
<i>Hepadnaviridae</i>	Duck hepatitis B viruses	Domestic duck (embryo) (<i>Anas platyrhynchos domesticus</i>)	Dead embryos	Histopathology	ND	Bidin et al., 2014
<i>Hepadnaviridae</i>	Goose hepatitis B viruses	Domestic goose (embryo) (<i>Anser domesticus</i>)	Dead embryos	Histopathology	ND	Bidin et al., 2014
<i>Herpesviridae</i>	Columbid herpesvirus 1BJ	Pigeon (<i>Columba livia domestica</i>)	Increased mortality, green faeces, emaciated, enlarged livers	In vivo pathogenicity; tissue distribution	ND	Zhang et al., 2015
<i>Parvoviridae</i>	Muscovy duck parvovirus	Muscovy duck (<i>Cairina moschata</i>)	Watery diarrhoea, respiratory signs, locomotory dysfunction	ND	ND	Zhu et al., 2014
<i>Parvoviridae</i>	Short beak and dwarfism syndrome virus M15	Mule duck (<i>Anas platyrhynchos</i> × <i>Cairina moschata</i>)	Short beak and dwarfism syndrome	In vivo pathogenicity	ND	Chen et al., 2016
<i>Picobirnaviridae</i>	Turkey picobirnaviruses, including GI/PBV/turkey/USA/MN-1/2011	Turkey (<i>Meleagris gallopavo</i>)	Light turkey syndrome	ND	Disease association study; prevalence; co-infections	Verma et al., 2015
<i>Picornaviridae</i>	Chicken phacovirus 1	Chicken (<i>Gallus domesticus</i>)	Diarrhoea	ND	Small prevalence study	Boros et al., 2016
<i>Picornaviridae</i>	Chicken proventriculitis virus isolate CPV/Korea/03	Chicken (<i>Gallus domesticus</i>)	Transmissible viral proventriculitis	Histopathology	ND	Kim et al., 2015
<i>Picornaviridae</i>	Siciniavirus JSY	Chicken (<i>Gallus gallus domesticus</i>)	Lethargy, tendency to huddle, decreased food and water intake, diarrhoea with white and green faeces, mortality	Gross pathology	Small prevalence study	Zhou et al., 2015
<i>Poxviridae</i>	Avipoxvirus XL, DX, TD	Mallard (<i>Anas platyrhynchos</i>)	Nodular lesions on the skin	Histopathology	Outbreak investigation	Zheng et al., 2015
<i>Poxviridae</i>	Turkey poxvirus-HU1124/2011	Turkey (<i>Meleagris gallopavo</i>)	Proliferative skin lesions	Histopathology	Outbreak investigation	Bányai et al., 2015
<i>Reoviridae</i>	Partridge reovirus strain D1007/2008	Partridge (<i>Perdix perdix</i>)	Pneumonia, infra-orbital sinusitis	ND	ND	Kugler et al., 2016
<i>Retroviridae</i>	Avian leucosis virus subgroup J viruses	Chicken (<i>Gallus gallus domesticus</i>)	Tumours, enlarged livers and spleens with milky white spots	Histopathology	ND	Dong et al., 2015

ND, no data available.

detected in a faecal sample collected from a chicken during an outbreak of mortality on a number of commercial chicken farms in China (Zhou et al., 2015). Clinical signs included lethargy, tendency to huddle, decreased food and water intake, and diarrhoea with white green faeces; morbidity was 50–80% and mortality was 30–50%. A small prevalence study indicated that infection with this novel virus was widespread, but the role of this virus in the mortality outbreak remained unclear. The third picornavirus, a megriovirus, was detected in the proventriculus of chickens during a

viral metagenomics study that was performed to elucidate a potential cause of transmissible viral proventriculitis in South Korea (Kim et al., 2015). However, the exact role of this virus in the disease could not be elucidated.

Novel viruses in domestic ducks

A number of novel viruses have been discovered in domestic ducks, with a clear association with disease. A novel avipoxvirus

was isolated in China during outbreaks of cutaneous nodules on the eyelids, beaks and legs in multiple domestic mallard duck flocks in China (Zheng et al., 2015).

In addition to a number of studies focussing on DTMUV (Wang et al., 2015; Zhu et al., 2015), a Tembusu-like flavivirus (Perak virus) was isolated from young Pekin ducks with neurological disease (Homonnay et al., 2014). This disease was observed on several farms in Malaysia in 2012 and was characterised by ataxia, lameness and paralysis. Phylogenetic analysis revealed that this virus was clearly distinct from other currently known tembusu-viruses and the role of this novel virus in the disease could be demonstrated by experimental inoculation of ducks, resulting in clinical signs and histological lesions similar to those in the natural disease (Homonnay et al., 2014).

Two novel parvoviruses have also been found in ducks in China. The first was a recombinant between a Muscovy duck parvovirus and a goose parvovirus, and was isolated from Muscovy ducklings with watery diarrhoea, respiratory signs and locomotory dysfunction (Zhu et al., 2014). The second was isolated from young Cherry Valley and mule duck flocks with short beak and dwarfism syndrome (SBDS), and was closely related to other goose parvoviruses isolated from mule ducks with SBDS (Chen et al., 2015, 2016).

In addition to these viruses, with which there was a clear association with disease, a Batai virus (family Bunyaviridae) of Africa-Asia lineage was isolated as part of an investigation into the presence of a possible viral agent that might be involved in a mild egg drop syndrome in Muscovy ducks on a farm in China (Table 3; see Appendix: Supplementary Table S1). However, experimental inoculation of ducks did not result in effective infection, since no virus or virus neutralising antibodies could be detected, and therefore the exact origin and role of this novel virus in the disease is currently unclear (Zhang et al., 2017).

Novel viruses in other domestic avian species

A novel avipoxvirus, detected in turkeys in Hungary in 2011, was associated with lesions of the skin and oral cavity (Bányai et al., 2015). Using viral metagenomics, various novel picobirnaviruses were identified in faeces from turkeys on farms with and without 'light turkey syndrome' in the USA; however, no significant differences in prevalence were observed between farms with and without the condition (Verma et al., 2015). The first partridge reovirus was isolated from dead birds on a partridge breeder farm in Hungary with increased mortality and infra-orbital sinusitis; this virus was composed of a mixture of sequences derived from chicken and turkey orthoreoviruses (Kugler et al., 2016) (Table 3; see Appendix: Supplementary Table S1).

Conclusions

Emerging viruses continue to have a major impact on the health of human beings and animals. To elucidate a possible viral origin of an idiopathic disease, viral metagenomics in combination with various other techniques is a useful approach. This is clearly demonstrated by a number of novel viruses that have been discovered in birds in the past few years, with a (potential) major impact on the health of various avian species. Some these viruses, or their variants, have the potential to spread to other animal species or humans. The number of viruses being discovered and characterised continues to increase, with each of them providing novel insights into the phylogenetic relationship of virus families, host ranges and tissue tropism.

The number of studies in which additional data has been collected to elucidate the pathogenic potential of novel viruses in birds is limited and the number of studies in which additional data

was collected to elucidate the impact of novel viruses on wild bird populations is even smaller. This highlights need to collect samples for epidemiological studies, especially for novel viruses detected in endangered species or with a potential zoonotic impact. Virus discovery in birds continues to provide interesting additional knowledge, but the most valuable information can only be obtained by intensive collaboration between multiple disciplines, including veterinarians, virologists, ecologists, conservation biologists, pathologists, bioinformaticians and epidemiologists.

Conflict of interest statement

The author of this paper has no financial or personal relationship with other people or organisations that could inappropriately influence or bias the content of the paper.

Appendix: Supplementary material

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.tvjl.2017.12.023>.

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