

Families of Viruses that Affect Passeriformes

Subjects: [Virology](#) | [Ornithology](#)

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Interest in emerging viruses is growing because some can cause serious or lethal disease in humans and animals. The number of cloacal virome studies is also growing, however, these usually focus on poultry and other domestic birds. These studies reveal a wide variety of viruses, although the pathogenic significance of most newly discovered viruses is uncertain. Analysis of viruses detected in wild birds is complex and often biased towards waterfowl because of the obvious interest in avian influenza or other zoonotic viruses. Less is known about the viruses present in the order Passeriformes, which comprises approximately 60% of extant bird species. This review aims to compile the most significant contributions, from traditional and metagenomic studies, on the viruses that affect passerines. It highlights most passerine species have never been sampled. Some viruses, especially Flaviviridae, Orthomyxoviridae, Poxviridae and Togaviridae, and arguably others, are considered emerging because of increased incidence or avian mortality/morbidity, spread to new geographical areas or hosts and their zoonotic risk. However, many of these viruses have only recently been described in passerines using metagenomics and their role in the ecosystem is unknown.

[biodiversity](#)[DNA viruses](#)[emergence](#)[metagenomic studies](#)[passeriformes](#)[RNAviruses](#)[spillover](#)[zoonoses](#)

1. Introduction

An emerging viral disease can be defined as a new occurrence of a disease because of: (a) the evolution or change of an existing virus or its spread to a new geographic area, species or ecological niche; (b) its rapidly increasing incidence, in terms of numbers of infected individuals or geographic range; or (c) a previously unrecognized disease or virus ^{[1][2][3][4][5]}. A viral disease of the past (i.e., one previously considered to be controlled) that re-appears with an increased prevalence in an area with susceptible host populations, expands its host range or appears in a new clinical form, is usually termed as re-emergent viral disease ^{[4][6]}. Many recent human emerging viral diseases have an animal origin, some with a significant impact on animal or public health, such as SARS-CoV-2, and two viruses that infect passerines: influenza A virus (AIV) and West Nile virus (WNV). The advent of modern, more powerful sequencing and bioinformatics technologies has increased the discovery of novel viruses in animals, with or without causing disease, that may be pathogenic, emergent, or zoonotic. Many of these novel and potentially emerging viruses are found in avian species that are present in virtually every ecosystem. Surprisingly, although passerines are the most abundant and diverse avian species worldwide, little is

known about the novel and emerging viruses that they host and their possible role in the emergence of new viral diseases in animals and humans.

Several factors are related to the development of emerging viruses and diseases as they enable infectious agents to evolve into new ecological niches, to reach and adapt to new hosts, and to spread more easily among the new hosts: urbanization and destruction of natural habitats, allowing humans and animals to live in close proximity; international travels and trade; climate change and changing ecosystems; changes in populations of reservoir hosts or intermediate insect vectors [4][5]. All these inter-dependent factors imply that the study of new or emerging viruses must be approached from a multisectoral and multidisciplinary perspective, framed in the One Health approach supported by the WHO, WOA and FAO [4][5] (**Figure 1**). The international trade of passerines, mainly ornamental breeds, has been also associated with the introduction of novel viruses in some countries, which pose a risk to native or endemic species if they can jump the species barriers, such as described with avipoxvirus in New Zealand [7]. There is also reasonable concern that more vulnerable individual species (of all taxa, including Passeriformes) may be at risk of extinction from viral pathogens. It is suggested that island endemic species are particularly vulnerable to pathogens, especially introduced pathogens to which they have no prior contact and no innate immunity [7]. Other authors have pointed out that all species with a small geographic range, low population size and low genetic diversity may be highly vulnerable to extinction, not just those island endemic species [8]. However, the researchers are not aware of any evidence that any species has ever become extinct due to a viral pathogen.

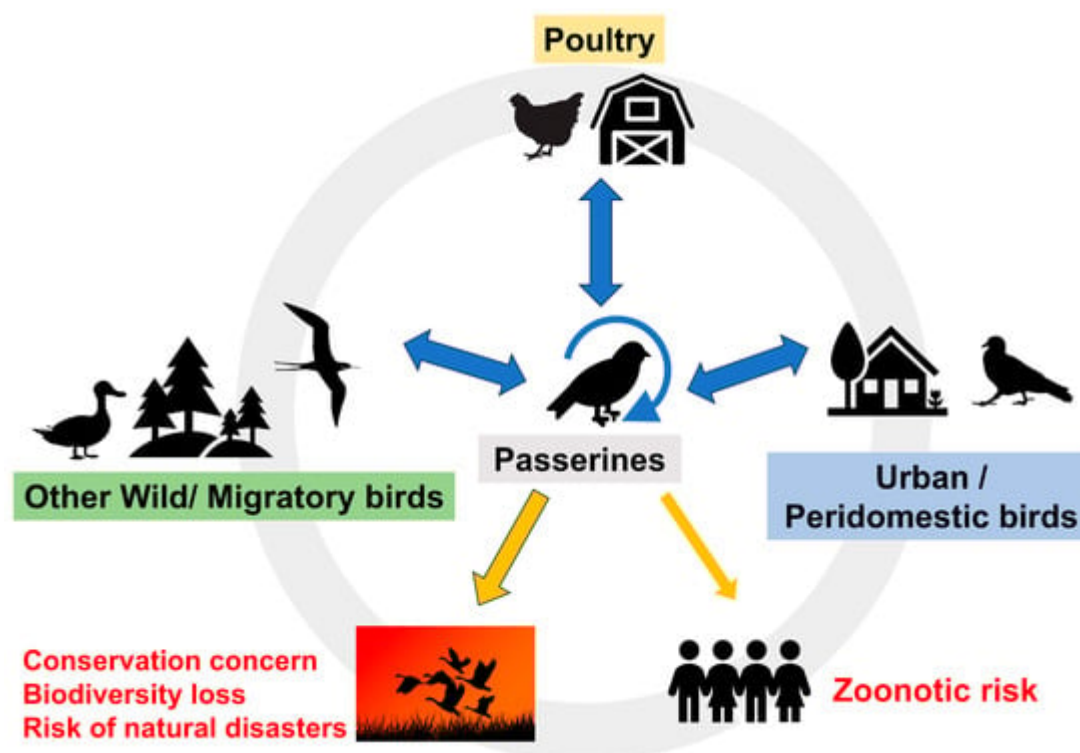


Figure 1. The theoretical role of passerine birds in the circulation and potential spillover of viruses and other infectious agents to other passerines (blue semi-circular arrow around the bird in the center), domestic, peridomestic and other wild birds (blue bidirectional arrows) and their relation to potential zoonotic risk or threats to

biodiversity (orange unidirectional arrows). The relation of passerines to theoretical consequences, such as zoonotic risk or threats to biodiversity, are depicted using orange unidirectional arrows. The One Health concept is represented by the light grey ring.

One of the most important factors that determines viral emergence is related to the adaptation of a given virus to new host species and/or the concomitant appearance of changes in the environment that offer new opportunities for the virus to thrive ^[9]. Some emerging viruses have a broad range of hosts. For example, RNA viruses such as West Nile virus (WNV) and Avian Influenza virus (AIV) can infect hundreds of different bird species including passerines. Others, such as herpesviruses or papillomavirus, are usually considered to be specific for one or a few related species ^{[9][10]}. Many species may act both as natural viral reservoirs and as amplifying hosts in bird-vector-bird cycles, for example, some togaviruses and flaviviruses. Occasionally these viruses are transmitted to incidental (dead-end) hosts including humans, equids, and other mammals. Birds can also act as a gene source of emerging viruses in cross-species transmission, for example, new influenza viruses may evolve through the reassortment of different gene segments ^[11].

The potential adaptation of an emerging virus to a new host depends on viral transmission routes (shedding of virus and infection in individuals) and the possibility of reaching this new host is facilitated by close and prolonged contact between individuals (such as breeding facilities). Viral transmission in birds may be horizontal (between individuals) or vertical (from females to offspring, congenitally or through embryonated eggs such as avian leukosis virus). Horizontal transmission is the most frequent and can occur by direct contact between animals (aerosols, fluids, feces, wounds or by predation or scavenging), by indirect contact through fomites or contaminated material (such as water, food, or troughs), and by vectors. Common vectors are blood-feeding arthropods such as mosquitos, midges, and ticks, in which the virus is propagated, and viruses transmitted mainly by this route are collectively called arboviruses (from Arthropod-Borne viruses). Vector-borne transmission is an indirect route of increasing importance in emerging viral diseases, some of which are important zoonoses, such as flaviviruses and togaviruses. It should be noted that viruses can be transmitted by more than one route.

Alternatively, viruses can enter the body via epithelial or the superficial mucosa of respiratory, gastrointestinal, and urogenital tracts. The most common routes of infection are ingestion of contaminated water or food (the fecal-oral route, for instance, picornaviruses) or inhalation of droplets expelled by an infected individual (respiratory route, for instance, herpesviruses and metapneumoviruses) or contaminated surfaces. Respiratory viruses can also be transmitted by contact with eye mucosa. In airborne transmission, viruses can spread over long distances through small respiratory aerosols that can remain suspended and travel in the air, such as influenza virus ^[12]. Viruses transmitted through ingestion usually are non-enveloped, resistant to low pH and to the acids in the digestive tract, and often produce diarrhea, causing large amounts of virus to be shed into the environment (where they can remain infectious for a long period of time) ^[9]. Diverse pathogens are probably transmitted between wild birds and domestic birds and poultry when feed and water are contaminated with feces in open aviaries and free-range farms. Describing the cloacal virome is essential for understanding the ecology of viruses circulating in the environment, identifying new virus-host relationships, and defining the risk of virus emergence ^[13]. However, data on the cloacal virome of wild or domestic passerines are still very scarce and, besides previous study in French

Guiana and Spain ^[13], there are only a few other studies in China ^{[14][15]} and Australia/New Zealand ^{[7][16][17]}. Increased investigation of the virome and emerging viruses of passerines is vital for predicting future outbreaks and spillovers that can affect birds and other animals, humans and biodiversity ^{[13][15]}.

Greater than two-thirds of viral taxa that infect humans are considered to be zoonotic: they are able to infect non-human vertebrates and may circulate in non-human reservoirs ^[18]. The alternative hosts for most zoonotic viruses are mammals (rodents, ungulates, other primates, carnivores, and bats). Birds are a much less important reservoir for zoonotic disease than mammals. Though less than 20% of zoonotic viruses share avian hosts ^[18], current data shows that birds are an important potential source for zoonotic viruses.

Passeriformes is the most diverse avian order. These are songbirds and perching birds with well-known species including sparrows, starlings, thrushes, magpies, crows, swallows, and finches. There are around 10,700 bird species, placed in 41 orders and 248 families, of which nearly 6400 species (59.6%) and 140 families (56.5%) are Passeriformes ^[19], making it by far the most speciose avian family. In addition, many passerine species are also extremely abundant. One recent estimate of the abundance of 92% of bird species determined that there are approximately 50 billion individual birds (albeit with high levels of uncertainty), of which 28 billion (56%) are Passeriformes ^[20]. This begs the question of whether the diversity of viruses circulating in Passeriformes is approximately equal to their share of avian diversity and abundance, and whether they could pose a significant risk to human and animal health and environmental balance.

Passerines include wild, urban, rural, and pet birds. Many passerine species are extremely abundant in the wild, but many populations of passerines are synanthropic species that live in close proximity to anthropogenic environments, which boosts the risk of the circulation of viral diseases between humans ^[21] poultry, and passerines (**Figure 1**). Pet passerines are usually bred for ornamental use, kept in captivity at home or in different types of aviaries (e.g., breeding facilities) that may have access to outdoors increasing the risk of contact with wild birds ^[22]. Migratory passerines can spread a wide variety of viruses over long distances, potentially being capable of infecting resident wild passerines (such as house sparrows, *Passer domesticus*), and these latter possibly contaminating pet birds living in open aviaries or poultry in farms ^[22]. For example, it has been suggested that small passerines could serve as bridge hosts for low-pathogenic avian influenza virus (LPAI) from infectious waterfowl to commercial turkey farms ^[23]. It is possible that the contact zone between agriculture and wildlife provides an interface where viruses could potentially circulate between wild and domestic birds ^[23] but probably vice versa as well. Passerines could play a larger role than previously thought in this interaction, a hypothesis that needs to be further studied.

2. Families of Viruses Affecting Passeriformes

The most important families of viruses affecting passerine birds are shown in **Figure 2**. Data on the bird species and families these viruses affect is summarized in **Table 1**, Tables S1 and S2 (can be downloaded at: <https://www.mdpi.com/article/10.3390/microorganisms11092355/s1>, Table S1: List of bird species; Table S2: List of avian families). Species recognized by the International Committee on Taxonomy of Viruses (ICTV) are italicized.

ROUTES OF VIRAL TRANSMISSION IN PASSERINES

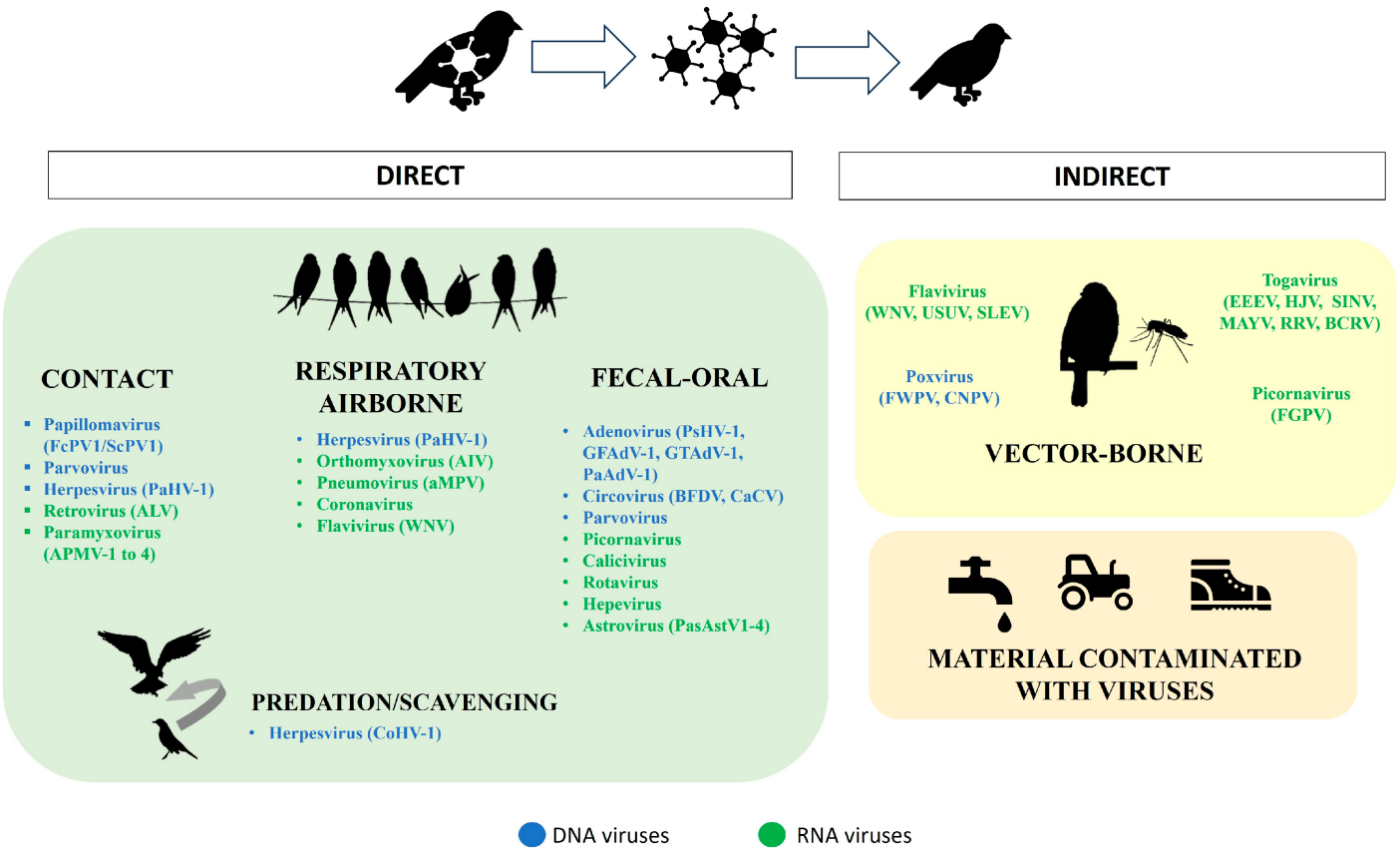


Figure 2. Viral transmission routes in passeriform birds. DNA viruses are shown in blue and RNA viruses in green. Avian Influenza virus (AIV), Avian leukosis virus (ALV), APMV (Avian paramyxovirus), APV (Avian papillomavirus), BCRV (Buggy Creek virus), BFDV (Circovirus), CaCV (Circovirus), CNPV (Canary poxvirus), CoHV-1 (Columbid herpesvirus-1), CoV (coronavirus), HEV (hepevirus), CRESS-DNA viruses (circular-rep encoded single stranded DNA), CV (calicivirus), EEEV (Equine eastern encephalitis virus), Estrildidae adenovirus (EsAdV), FcPV (Fringilla coelebs papillomavirus), FGPV (Picornavirus), FWPV (Fowlpox virus), GFAdV-1 (Gouldian finch adenovirus-1), GTAdV-1 (great tit adenovirus-1), HPAI (Highly pathogenic Avian Influenza), HJV (Highland J virus), MAYV (Mayaro virus), PaHV-1 (Passerid herpesvirus-1), PaPV (Passerid parvovirus), PasAstV (Passerid astrovirus), Passerid adenovirus-1 (PaAdV-1), PsHV-1 (Psittacid herpesvirus-1), RRV (Ross River virus), RVA (rotavirus), ScPV1 (Serinus canaria papillomavirus), SINV (Sindbis virus), SLEV (Saint Louis Encephalitis virus), USUV (Usutu virus), and WNV (West Nile virus).

Table 1. Virus names, abbreviations and genus/species designations are listed according to the taxonomy and nomenclature approved by the International Committee on Taxonomy of Viruses (ICTV) [24]. All ICTV accepted viral taxa are in italics.

Viral Family	Genus	Viral Taxa	Abbreviations	Nomenclature	Bird Family	Clinical Signs	Mortality Rate	References
dsDNA VIRUSES								

Viral Family	Genus	Viral Taxa	Abbreviations	Nomenclature	Bird Family	Clinical Signs	Mortality Rate	References
Herpesviridae	Iltovirus	Gallid herpesvirus 1	GaHV-1	Iltovirus gallidalpha1	Turdidae, Estrildidae, Sturnidae	Subclinical infection/ Respiratory signs	High	[7] [25] [26] [27] [28]
		Psittacid herpesvirus 1	PsHV-1	Iltovirus psittacidalpha1	Sturnidae			
		passerid herpesvirus 1		not recognized	Fringillidae			
	Mardivirus	Columbid herpesvirus 1	CoHV-1	Mardivirus columbidalpha1	Corvidae, Turdidae	Subclinical infection	Probably not	[29]
Poxviridae	Avipoxvirus	Fowlpox virus (Lineage A1)	FWPV	same	Fringillidae, Passeridae	Cutaneous lesions/Upper respiratory and digestive tract lesions	High	[30] [31] [32] [33] [34] [35] [36] [37] [38] [39] [40] [41] [42]
		Pigeonpox virus (Lineage A2)	PGPV	same	Fringillidae		High/Medium	
		Accipitriformespox virus (Lineage A7)		same	Lanidae		High/Medium	
		Canarypox virus (Lineage B1)	CNPV	same	Fringillidae, Paridae, Corvidae (and 11 other families)		High/Medium	
		Starlingpox virus (Lineage B2)		same	Sturnidae, Passeridae		High/Medium	
		Lineage B3 poxvirus		not recognized	Corvidae (and eight other mostly Passeriformes families)		High	
		Atadenovirus	European robin adenovirus		not recognized		Meliphagidae, Fringillidae, Ploceidae, Estrildidae, Turdidae, Ptilonorhynchidae, Sturnidae, Zosteropidae, Maluridae, Petroicidae	
Adenoviridae	Atadenovirus	European greenfinch adenovirus		not recognized				
		Eurasian siskin adenovirus		not recognized				
		Eurasian bullfinch adenovirus		not recognized				
		common chaffinch		not recognized				

Viral Family	Genus	Viral Taxa	Abbreviations	Nomenclature	Bird Family	Clinical Signs	Mortality Rate	References
		adenovirus						
		passerine adenovirus 1		not recognized				
		white plumed honeyeater adenovirus 1, -2		not recognized				
		vitelline masked weaver adenovirus strains 37869 and 38132		not recognized				
	Aviadenovirus	great tit adenovirus strain 47292		not recognized				
		european greenfinch adenovirus		not recognized	Fringillidae, Estrildidae, Paridae, Ploceidae, Sylvidae, Falcunculidae, Petroicidae	Subclinical infection/ Not known	Probably not	
		goldfinch adenovirus		not recognized				
		vitelline masked weaver adenovirus strain 39658		not recognized				
		double-barred finch adenovirus		not recognized				
	Siadenovirus	eurasian blackcap adenovirus		not recognized	Estrildidae, Paridae, Sylvidae, Thraupidae, Meliphagidae, Pardalotidae, Rhipiduridae, Sturnidae	Subclinical infection/ Probable renal lesions	Probably not	[45] [46]
		gouldian finch adenovirus 1	GFAdV-1	not recognized				
		great tit adenovirus strain 47292	GTAdV-1	<i>Great tit siadenovirus A</i>				
		zebra finch adenovirus strain 47535		not recognized				
Papillomaviridae	Etapapillomavirus	<i>Fringilla coelebs Papillomavirus 1</i>	FcPV1	<i>Etapapillomavirus 1</i>	Fringillidae	Cutaneous lesions	Low	[47] [48] [49] [50] [51] [52]

Viral Family	Genus	Viral Taxa	Abbreviations	Nomenclature	Bird Family	Clinical Signs	Mortality Rate	References
ssDNA VIRUSES		Serinus canaria papillomavirus 1	ScPV1	not recognized	Fringillidae	Not known	Not known	[53]
Circoviridae	Circovirus	Beak and feather disease virus	BFDV	Circovirus parrot	Artamidae, Corvidae, Estrildidae, Fringillidae, Petoicidae, Sturnidae, Thamnophilidae	Feather lesions	Probably not	[54][55][56]
		Circovirus canary	CaCV	same		Feather diseases and immunosuppression/ Subclinical infection	Yes/Not known	[57][58][59][60][61]
		Circovirus finch	FiCV	same				
		Circovirus raven	RaCV	same				
		Circovirus starling	StCV	same				
		Circovirus zebrafinch	ZfiCV	same				
	Cyclovirus	Robinz virus RP_736	RobinzV736	Cyclovirus cervienka	Petroicidae	Not known	Not known	[17]
		Robinz virus RP_1170	RobinzV1170	Cyclovirus liepsnele				
		Robinz virus RP_493	RobinzV493	Cyclovirus pettirosso				
		Robinz virus RP_620	RobinzV620	Cyclovirus prihor				
		Robinz virus RP_526	RobinzV526	Cyclovirus punarinta				
		Robinz virus RP_584	RobinzV584	Cyclovirus rudzik				
		Robinz virus RP_259	RobinzV259	Cyclovirus totoï				
	Probably new genus	Gyrovirus 11		not recognized	Thamnophilidae	Not known	Not known	[62]
Genomoviridae	Gemycirculavirus	new species		not recognized	Petroicidae, Aegithalidae, Corvidae, Emberizidae, Fringillidae, Muscicapidae, Paridae,	Not known	Not known	[63]

Viral Family	Genus	Viral Taxa	Abbreviations	Nomenclature	Bird Family	Clinical Signs	Mortality Rate	References			
		Chickadee associated gemycircularvirus 1		Gemycircularvirus chickad1	Paridae			[64]			
		Finch associated genomovirus 5		Gemycircularvirus haeme1	Fringillidae			[65]			
		Finch associated genomovirus 6		Gemycircularvirus haeme2				[65]			
	Gemykibivirus	Blackbird associated gemykibivirus 1		Gemykibivirus blabi1	Turdidae					[66]	
		Black robin associated gemykibivirus 1		Gemykibivirus blaro1	Petroicidae						
		Finch associated genomovirus 3		Gemykibivirus haeme1	Fringillidae						
		Finch associated genomovirus 2		Gemykibivirus haeme3							
		Finch associated genomovirus 4		Gemykibivirus haeme4						[65]	
		Finch associated genomovirus 1		Gemykibivirus haeme5							
		Gemykroznavirus	Finch associated genomovirus 8		Gemykroznavirus haeme1					Fringillidae	[66]
		Gemygorvirus	Starling associated gemygorvirus 1		Gemygorvirus stara1					Sturnidae	
Parvoviridae	Aveparvovirus	Aveparvovirus passeriform1	PfPV	same	Thraupidae	Not known	Not known	[67]			
ssRNA VIRUSES											
Orthomyxoviridae	Alphainfluenzavirus 1	Highly Pathogenic Avian Influenza H5N1	FLUAV/(H5N1)	Alphainfluenzavirus influenzae	Passeridae, Turdidae, Ploceidae,	Mild/Severe disease	High	[68] [69] [70] [71] [72] [73]			

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Viral Family	Genus	Viral Taxa	Abbreviations	Nomenclature	Bird Family	Clinical Signs	Mortality Rate	References
Paramyxoviridae					Corvidae, Hirundinidae, Icteridae (and many other families)			[74] [75] [76] [77]
	Orthoavulavirus	Avian paramyxovirus 1 (NDV, Newcastle Disease virus)	APMV-1	Orthoavulavirus javaense	Passeridae, Motacillidae, Passarellidae	Not known/Subclinical disease		[78] [79] [80] [81] [82]
	Metaavulavirus	Avian paramyxovirus 2	APMV-2	Metaavulavirus yucaipaense	Corvidae, Motacillidae, Troglodytidae, Muscicapidae, Emberizidae, Estrildidae	Mild/Severe disease	High/Not known	[83] [84] [85] [86] [87] [88] [89]
	Paraavulavirus	Avian paramyxovirus 3	APMV-3	Paraavulavirus wisconsinense				[90] [91]
	Paraavulavirus	Avian paramyxovirus 4	APMV-4	Paraavulavirus hongkongense				[92]
Pneumoviridae	Metapneumovirus	Avian metapneumovirus	AMPV	Metapneumovirus avis	Passeridae, Sturnidae	Not known	Not known	[93] [94]
Bornaviridae	Orthobornavirus	Estrildid finch bornavirus 1	EsBV-1	Orthobornavirus estrildidae	Estrildidae, Corvidae, Fringillidae	Not known	Not known	[95] [96] [97] [98]
		Canary bornavirus 1	CnBV-1	Orthobornavirus serini				
		Canary bornavirus 2	CnBV-2					
		Canary bornavirus 3	CnBV-3					
Flaviviridae	Orthoflavivirus ¹	Japanese encephalitis virus	JEV	Orthoflavivirus japonicum	Passeridae, Corvidae, Fringillidae, Turdidae (and >23 more families)	Not known	High	[99] [100] [101] [102] [103]
		Saint Louis encephalitis virus	SLEV	Orthoflavivirus louisense				
		Murray Valley Encephalitis virus	MVEV	Orthoflavivirus murrayense	[104]			
		Usutu virus	USUV	Orthoflavivirus usutuense	Severe disease	[105] [106] [107]		
		West Nile virus	WNV	Orthoflavivirus nilense	Mild/Severe disease	[108] [109] [110] [111]		

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	Viral Family	Genus	Viral Taxa	Abbreviations	Nomenclature	Bird Family	Clinical Signs	Mortality Rate	References	Discovery		
1	and Emergence Ph					Sci 2012		2871	[112] [113]			
1	Togaviridae	Alphavirus ¹	Eastern equine encephalitis virus	EEEV	same	Turdidae, Hirundidae, Icteridae, Petroicidae, Estrildidae, Monarchidae	Neurological disease	Yes	[114] [115] [116]	C.		
			Highlands J virus	HJV	same		Mild disease		[117]			
			Sindbis virus	SINV	same		Severe disease		[118] [119]			
			Ross River virus	RRV	same		Not known		[120] [121]			
2			Mayaro virus	MAYV	same				[122] [123] [124] [125]			
2		Deltacoronavirus ²	Buggy Creek virus	BUCGV	Fort Morgan virus	Turdidae, Estrildidae, Pycnonotidae, Passeridae, Zosteropidae, Fringillidae, Emeberizidae	Neurological disease	Probably high	[126] [127] [128]	K.E. 198–402. New and skyard		
2			Bulbul coronavirus HKU11	BulCV_HKU11	same		Severe disease		[129] [130] [131]			
2			Munia coronavirus HKU13	MunCV_HKU13	same							
2			Thrush coronavirus		not recognized							
2	Picornaviridae	Oscivirus	White-eye coronavirus HKU16	WECov_HKU16	same	Turdidae, Muscicapidae	Severe disease	Not known	[132] [133]	Terbini, my		
2			Coronavirus HKU15	PoCoV_HKU15	same							
2			Oscivirus A1 and A2 (turdivirus 2 and 3)	OsV-A1/OsV-A2	Oscivirus A							
2			Passerivirus A and B	PasV-A/PasV-B	same							
2		Poecivirus	Poecivirus A1	PoeV-A	Poecivirus A	Paridae		Yes	[134] [135]	3.		
2	Astroviridae	Avastovirus	Probably new genus	French Guiana Picornavirus	FGPV	not recognized	Thamnophilidae	Not known	Not known	[13]	f a virus	
			novel avastrovirus clades 4 and 5		not recognized	Fringillidae, Monarchidae Parulidae, Passeridae	Subclinical infectionMild disease	Not known	[136] [137] [138]			

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Viral Family	Genus	Viral Taxa	Abbreviations	Nomenclature	Bird Family	Clinical Signs	Mortality Rate	References
<i>Caliciviridae</i>	Probably new genera	new calicivirus		not recognized	Prunellidae, Turdidae, Emberizidae, Fringillidae, Muscicapidae, Petroicidae	Subclinical infection	Not known	(7) (15) (139) (140)
<i>Hepeviridae</i>	Probably new genera	new hepe-like viruses		not recognized	Thamnophilidae, Turdidae, Zosteropidae	Not known	Not known	(7) (13) (15)
dsRNA VIRUSES								
<i>Reoviridae</i>	<i>Orthoreovirus</i> ²	new orthoreovirus		not recognized	Emberizidae, Turdidae, Fringillidae	Not known	High mortality	(141) (142)
RNA REVERSE TRANSCRIBING VIRUS								
<i>Retroviridae</i>	<i>Alpharetrovirus</i>	<i>Avian leukosis virus</i>	ALV	same	Emberizidae, Paridae, Corvidae, Muscicapidae, Thraupidae, Phylloscopidae	Subclinical infection	Possibly	(143) (144) (145)

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