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Tsiodras, Sotirios Kelesidis, Theodoros Kelesidis, Iosif et al.

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REVIEW

Human infections associated with wild birds

Sotirios Tsiodras a,*,g, Theodoros Kelesidis b,g, Iosif Kelesidis b, Ulf Bauchinger c,f, Matthew E. Falagas d,e

- ^a University of Athens Medical School, 1 Rimini Street, Xaidari, 12462 Athens, Greece
- ^b Beth Israel Deaconess Medical Center, Harvard University Medical School, Boston, MA, USA
- ^c University of Munich (LMU), Planegg-Martinsried, Germany
- ^d Alfa Institute of Biomedical Sciences, Athens, Greece
- e Department of Medicine, Tufts University School of Medicine, Boston, MA, USA

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Arbovirus;
West Nile encephalitis;
Enteric infection;
Antimicrobial
resistance

Summary Introduction: Wild birds and especially migratory species can become long-distance vectors for a wide range of microorganisms. The objective of the current paper is to summarize available literature on pathogens causing human disease that have been associated with wild bird species.

Methods: A systematic literature search was performed to identify specific pathogens known to be associated with wild and migratory birds. The evidence for direct transmission of an avian borne pathogen to a human was assessed. Transmission to humans was classified as direct if there is published evidence for such transmission from the avian species to a person or indirect if the transmission requires a vector other than the avian species.

Results: Several wild and migratory birds serve as reservoirs and/or mechanical vectors (simply carrying a pathogen or dispersing infected arthropod vectors) for numerous infectious agents. An association with transmission from birds to humans was identified for 10 pathogens. Wild birds including migratory species may play a significant role in the epidemiology of influenza A virus, arboviruses such as West Nile virus and enteric bacterial pathogens. Nevertheless only one case of direct transmission from wild birds to humans was found.

Conclusion: The available evidence suggests wild birds play a limited role in human infectious diseases. Direct transmission of an infectious agent from wild birds to humans is rarely identified. Potential factors and mechanisms involved in the transmission of infectious agents from birds to humans need further elucidation.

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f Mitrani Department of Desert Ecology, Ben-Gurion University of the Negev, Ben-Gurion, Israel

^{*} Corresponding author. Tel.: +30 210 5831989, +30 6932 665820; fax: +30 210 5326446. *E-mail address*: tsiodras@med.uoa.gr (S. Tsiodras).

^g The first two authors contributed equally to this work.

Introduction

Free-living birds, including migratory species, can become long-distance vectors for a wide range of microorganisms that can be transmissible to humans. 1 This creates the potential for establishment of novel foci of emerging or re-emerging communicable diseases along bird migration routes.² Certain pathogens are more often isolated in migratory birds in comparison to other animal species^{3,4} and the potential for transport and dissemination of these pathogens by wild birds is of increasing public health concern stimulated by the recent spread of diseases like highly pathogenic Avian influenza A (HPAI H5N1 Asian lineage) and West Nile virus (WNV) infection.3,5 Avian influenza A (HPAI H5N1 Asian lineage) and West Nile virus infection, well known to affect birds for decades, have been recently observed to affect areas far away from the locations where they were originally identified, generating the hypothesis that migratory birds transported these pathogens to new geographical locations. However as is the case with the highly pathogenic avian influenza, scientific data do not always support such hypotheses.⁷ Several factors affecting wild bird species including migratory species such as increasing stress levels and crowding potentially promote infectious disease transmission among birds but available data supporting this are scarce or nonexistent.

The objective of this paper is to summarize available literature on pathogens causing human disease that have been associated with wild birds including wild migratory bird species. Although wild bird borne infections can occur at any spatial scale, from very localized, to short and long distance, from an epidemiologic point of view the transmission of pathogens from wild birds to humans over a long distance is most important. Therefore, in the current manuscript we focused more on the role of wild migratory birds in the spread of certain pathogens. The paper focuses on available evidence of transmission of avian borne pathogens to humans. We speculated that such evidence would originate from enhanced animal and human surveillance and the application of advanced molecular diagnostic testing during the recent years. Furthermore, we attempted to identify factors potentially contributing to such transmission from the available body of science.

Methods

Two reviewers (TK and IK) independently performed the literature search. The following terms were used in searches of the PubMed database: "wild birds", "imgratory birds", "infection", and specific pathogens known to be associated with wild and migratory birds e.g. "West Nile virus", "avian influenza", "influenza A", "Lyme disease" and "arbovirus". We also screened articles related to the initially identified publications to expand our data sources. Despite the availability of scientific data on this issue even before 1966^{8,9} we focused in the modern area where molecular diagnostics might enhance our ability to study such interactions between birds and humans. Similar searches were conducted for each individual migratory

bird species identified through a list provided by the Royal Ornithological Society of Great Britain and World bird databases (Avibase World List). 10,111 We also used the widely used Sibley and Monroe Classification for birds. 12,13 To evaluate the role of recent diagnostic developments, we also performed an additional search of the literature by using the term polymerase chain reaction (PCR) and "migratory birds". Additional epidemiologic information for the identified pathogens-diseases was obtained from the websites of the United States Centers for Disease Control (CDC), World Health Organization (WHO), FAO, and OIE. 14,15

Study selection and data extraction

The role of wild and migratory birds in the transmission of an infectious disease to humans was discussed in consensus meetings where all authors participated. Transmission to humans was classified as direct if there was evidence for direct transmission of the pathogen from the avian species to humans through direct contact with an infected bird and genetic/serological evidence of the presence of a particular pathogen in both the avian species and humans. Transmission to humans was classified as indirect if there was evidence for transmission of the pathogen from the avian species to humans through indirect contact with an infected bird and genetic/serological evidence of the presence of the particular pathogen in both the avian species and humans. We considered indirect ways of transmission, those through contaminated water from feces of waterfowls and through vectors that are carried by wild birds such as mosquitoes and ticks (Table 1). Finally, we classified pathogens to be associated with a "theoretical risk for transmission" when in the literature there were reports that these pathogens were isolated both from humans and wild birds, using microbiological, genetic or serological methods, but there were no reports of actual direct/indirect transmission of these pathogens from wild birds to humans. Despite the lack of actual evidence in such cases, the risk exists in theory e.g. through ingestion of water contaminated from feces of wild birds or exposure to inanimate surfaces contaminated by bird secretions or droppings.

Compiled relevant bird species data (with formal avian family names) are presented in the appendix. This appendix further includes data on pathogens that are borne by wild avian species that have not yet been associated with human infection in published reports.

Results

Evidence for direct transmission

The systematic review of the literature review identified no real evidence for direct wild bird to human transmission with the only exception being the cluster of H5N1 human cases in Azerbaijan where the affected patients were plucking feathers from mute swans that had succumbed to H5N1 infection. ¹⁶

Microorganism(s)	Reported transmission to human (indirect transmission) ($n = 10$)	Migratory bird species (formal family names for each bird species can be found in the appendix)	Geographic area
(I) Bacteria			
Chlamydiaceae Chlamydophila psittaci	Ornithosis ^{17—22}	Egrets (Ardea Alba), grackles (Quiscalus), gulls (Larus), migratory waterfowl species (Anatidae), passerines (Passeriformes), pigeons (Columbidae), psittacine birds (Psittaciformes), raptors (North American raptors), shorebirds (North American shorebirds), wild ducks (Anatidae), and others	Worldwide
Enterobacteriaceae			
Escherichia coli Salmonella	Bloody diarrhea [Vero cytotoxin- producing E. coli O157, Shiga toxin stx2f- containing E. coli O128 strain) ^{23,24}] ^{25,26} Salmonellosis (enteritis) ^{27–30}	Finches (Fringillidae), gulls (Larus), pigeons (Columbidae), sparrows (Passeridae), starlings (Sturnidae) Wild crows (Corvidae), ducks	Worldwide Worldwide
(enterica typhimurium)	Jamonettosis (entericis)	(Anatidae), gulls (Larus), passerines (Passeriformes), raptorial birds (North American raptors), songbirds (Passeriformes), terns (Sternidae), waterfowls (Anatidae)	wortdwide
Mycobacteriaceae			
Mycobacterium (avium, ulcerans)	Regarding <i>M. avium</i> it is generally believed and occasionally reported that man (especially immunocompromised, elderly) can contract the disease from birds, but this has not been fully clarified. ^{31–33} Possible transmission of <i>M. ulcerans</i> to humans through contaminated water from feces of waterfowls (<i>Anatidae</i>) ³⁴	Crows (Corvidae), raptors (North American raptors), rooks (Corvus frugilegus), wild ducks (Anatidae), wild pigeons (Columbidae)	Worldwide
Spirochaetaceae	Lyme disease ^{30,35–41}		
Borrelia burgdorferi sensu lato genomic species		American Robins (<i>Turdus migratorius</i>), cardinals, songbirds (<i>Passeriformes</i>), sparrows (<i>Passeridae</i>), thrushes (<i>Turdidae</i>) and other ground foraging birds, waterfowl (<i>Anatidae</i>)	North America Europe
(II) Fungi			
Cryptococcus	Yes (wild pigeons) ^{42–46}	Psittacine birds (<i>Psittaciformes</i>), starling (<i>Sturnidae</i>), wild pigeons (<i>Columbidae</i>)	Europe, South America, Asia
(III) Viruses			
Flaviviridae			
West Nile virus	Yes ^{3,30,47–49}	North American shorebirds, common grackles (<i>Quiscalus quiscula</i>), doves, hawks, house finches (<i>Carpodacus mexicanus</i>), and house sparrows (<i>Passer domesticus</i>), songbirds (<i>Passeriformes</i>), raptors (North American raptors), owls (<i>Strigidae</i>), and various corvids (crows, jays, <i>Corvidae</i>)	Africa Europe, Asia, America
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Microorganism(s)	Reported transmission to human (indirect transmission) $(n = 10)$	Migratory bird species (formal family names for each bird species can be found in the appendix)	Geographic area
St. Louis encephalitis virus (SLEV)	Yes ^{3,49–51}	North American shorebirds, common grackles (<i>Quiscalus</i>), doves, hawks, house finches (<i>Carpodacus mexicanus</i>), and house sparrows (<i>Passer domesticus</i>), songbirds (<i>Passeriformes</i>), owls (<i>Strigidae</i>), and various corvids (crows, jays, magpies)	America
Western Equine Encephalitis virus (WEEV)	Yes ⁴⁹	North American shorebirds, quails (Coturnix)	America
Orthomyxoviridae Influenza A virus	To date, only domestic poultry are known to have played a major role in the transmission cycle of the H5N1 virus from animals to humans. However, there is also the potential contribution of other hosts like carnivores e.g cats to both virus transmission and adaptation to mammals. Head or moribund cats were found to be infected with H5N1 virus soon after the virus was detected in wild birds in Germany. Head or moribund cats were found to be transmitted from wild birds to cats whereas in another report avian influenza A virus subtype H5N1 was transmitted to domestic cats by close contact with infected birds. However, there has been no documented case with wild migratory bird to human transmission although the theoretical risk exists. Serologic evidence of avian influenza infection in 1 duck hunter and 2 wildlife professionals with extensive histories of wild waterfowl (Anatidae) and game bird exposure has been reported. Here is an association (not necessarily causal) between recreational contact with H5N1 contaminated water and the onset of confirmed human H5N1 disease in 3 cases. As symptomatic ducks may have shed virus into the pond. San Possible direct transmission of highly pathogenic avian influenza in family cluster in Azerbaijan. Cocupational exposure to avian species may increase veterinarians' risk of avian influenza virus infection. Services of avian influenza virus infection, keratoconjuctivitis, diarrhea, encephalitis And of the services of avian influenza virus infection, keratoconjuctivitis, diarrhea, encephalitis And of the services of avian influenza virus infection, keratoconjuctivitis, diarrhea, encephalitis And of the services of avian influenza virus infection, keratoconjuctivitis, diarrhea, encephalitis And of the services of the services of the services of avian influenza virus infection, keratoconjuctivitis, diarrhea, encephalitis And of the services of the services of avian influenza virus infection.	Dabbling ducks (e.g common Mallard-Anas platyrhynchos), geese (Anserinae), gulls (Larus), swans (Cygninae), guillemots (Uria aalge), mountain hawk eagles (Spizaetus nipalensis) North American Bluewinged Teal (Spatula discors), shearwaters (Procellariidae), terns (Sternidae). Wild aquatic birds are regarded as the principal reservoir of influenza viruses, and migrating ducks (Anatidae) disseminate influenza viruses worldwide	Worldwide

Evidence for indirect transmission or a theoretical risk for transmission

Although a large number of avian borne pathogens have been identified in the literature, we found relatively scarce evidence for indirect transmission of avian borne pathogens to humans (Table 1). Unfortunately, in the vast majority of the reports reviewed herein, data were unavailable to further characterize the way of transmission of certain pathogens beyond the stage of a speculative argument. This would be expected for zoonoses which usually require amplification in an animal species cycle before spill-over to humans. Nevertheless and based on our criteria several avian borne bacterial, fungal, viral pathogens could be indirectly transmitted or associated with a theoretical risk for transmission to humans (Table 1). We identified 58 such pathogens for which wild birds can serve as reservoirs, mechanical vectors, or both (Tables 1 and 2). However, the paucity of available data did not allow us to make the distinction whether the involved species serve as reservoir or vector in most of the cases.

Scarce microbiological, serological and epidemiological data supported indirect transmission from wild birds to human for 10 of these pathogens (Table 1). Application of advanced molecular diagnostic testing during the recent years has led to the isolation of these microbial agents known to affect humans in birds. The examples include bacterial spp. like Escherichia coli, ^{24,25} Borrelia Burgdorferi, ³⁷ Anaplasma phagocytophilum, ⁸⁷ Salmonella typhimurium, ²⁸ Campylobacter spp., 79 and Mycobacterium spp., 31-33 viruses like *Influenza* virus, ^{56,60,61,64,65} *West Nile* virus, ¹²⁶ *St. Louis encephalitis virus* ^{3,50,51} and *Western Equine En*cephalitis virus⁴⁹ and fungi like Cryptococcus spp..^{43,44,46} These have been isolated from many wild birds using standard serological^{3,30,47,48,50,51,56,60,61,64,65,79} and microbiotechniques. 28,31–33,37,43,44,46,79,126,127 vectors with the ability to carry pathogens have also been isolated from wild birds. ^{3,37,85,87} For example, ornithophilic mosquitoes and ticks are the principal vectors of pathogens like West Nile virus in the Old World, and B. burgdorferi, respectively, and birds of several species, chiefly migrants, appear to be the major introductory or amplifying hosts of these vectors. 3,37,85,87

Methods that have been used to confirm association of microbial agents isolated from wild birds with infection in humans include molecular methods like sequence analysis for *Ehrlichia*⁸⁵ and *Mycobacterium* species, ^{32,33} phylogenetic analysis, ²⁵ pulsed-field gel electrophoresis, ²⁶ polymerase chain reaction, ²⁶ immunomagnetic separation (IMS) for *E. coli*, ^{25,26} serological methods for influenza virus ^{56,59} and psittacosis, ¹⁷ and epidemiological methods for *Salmonella* spp., ^{28,29} *Borrelia* spp., ³⁶ *West Nile virus*, ^{30,48,49,126} *St. Louis encephalitis virus*, ^{49,51} and *Western Equine Encephalitis virus*.

However, in most scientific literature, there is no detailed data regarding the detection and characterization of pathogens and their relation to wild birds. In most of the cases, it seems that wild birds serve as vectors of the pathogen. In these cases, the indirect role of wild birds in transmission of the infectious agents can be only speculated and the implicated pathogens are classified as having

the theoretical risk of transmission from wild birds to humans (Table 2).

Twenty-one wild avian family species were identified that are reservoirs, mechanical vectors or both for infectious agents that may affect humans (Listed with their formal family names in the appendix according to the Sibley and Monroe Classification for birds). A short description of pathogens that may be transmitted from wild birds to humans is outlined below.

Types of microorganisms carried by wild birds that could affect humans (indirect transmission or theoretical risk)

Bacteria

A range of bacterial pathogens affecting humans has been associated with wild and migratory birds. An indirect transmission to humans has been reported for some of these such as the enteric pathogens *E. coli*²⁴ and *Salmonella* spp. ^{28,29} Tick-borne pathogens such as *Borrelia burg-dorferi sensu lato* species have been also associated with human infection from wild migratory birds. ^{35–38,85,87} A theoretical risk for transmission to humans has been reported for other bacterial pathogens such as *Yersinia* spp., ^{76,128} *Campylobacter jejuni*⁷⁷ and both cholera and non-cholera *Vibrio* spp. ⁹²

Fungi

Yeasts and yeast-like fungi have been isolated from wild and migratory birds such as *Candida* spp., ^{129,130} and hyphomycetes e.g. *Aspergillus* spp., *Microsporum* spp., *Trichophyton* spp., ¹¹² and cryptococci. ⁴³ A theoretical risk for transmission to humans exists but scientific data to support this are extremely scarce. Cryptococci that are quite ubiquitous in nature have been reported to be transmitted to humans indirectly from wild pigeons (*Columbidae*), occasionally causing clinical infection, especially in immunocompromised patients. ⁴²

Viruses

Important viral species have been isolated from wild migratory birds and can affect humans indirectly including *influenza A viruses*, ^{62,131} the *West Nile virus* (WNV), ^{3,47} the *St. Louis encephalitis virus* (SLEV). ^{3,50,51} Several other viral species can theoretically be transmitted from wild birds to humans (Table 2).

Parasites

Wild and migratory birds can disperse in nature a diverse number of protozoa such as *Babesia* and other haemoparasites. The potential for transmission exists for some parasitic species (Table 2).

Factors potentially contributing in transmission

The issue of the transmissibility of various pathogens from wild birds including migratory species to humans is fairly complex. Several factors determine the possibility of such a spread. Some factors relate to the affected species including the birds themselves (e.g. the avian species involved, susceptible local vertebrate recipients or

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Microorganism(s)	Potential for transmission to humans exists $(n = 50)$	Migratory bird species	Geographic area
(I) <i>Bacteria</i> Gram-positive cocci			
Enterococcus	Possible spread through polluted water ^{67,68} ; transmission has been reported from other birds ^{69–71}	Ducks (Anatidae), seagulls (Larus), waterfowls (Anatidae) and other migratory birds such as quails (Coturnix)	Worldwide
Staphylococcus	Possible through faecal pollution of environmental water samples ⁷²	Ducks (Anatidae), mallards (Anas platyrhynchos), passerines (Passeriformes), seagulls (Larus), and other migratory birds including quails (Coturnix), raptors (North American raptors)	Worldwide
Gram-positive rods			
Clostridium perfringens	Possible through accidental ingestion of contaminated water ⁷³ ; food-borne enteritis has been reported from non-migratory birds ⁷⁴	Crows (<i>Corvidae</i>), ducks (<i>Anatidae</i>), gulls(<i>Larus</i>), Pelicans (<i>Pelecanus</i>) and marine birds, raptors (North American raptors), shorebirds (North American shorebirds), waterfowls (<i>Anatidae</i>)	Europe, Asia
Listeria monocytogenes	Possible through accidental ingestion of contaminated water ⁷⁵	Crows (corvus), gulls (Larus), rooks (Corvus frugilegus) and other migratory birds	America, Asia
Enterobacteriaceae <i>Yersinia</i> species	Enteritis ^{30,76}	Crows (corvus), ducks (Anatidae), gulls (Larus), magpies, (Corvidae) pigeons (Columbidae), pheasants, starlings (Sturnidae), terns (Sternidae), wagtails (Motacilla), waterfowls (Anatidae) and other migratory species	Worldwide
Campylobacteraceae			
Campylobacter jejuni	Intestinal campylobacteriosis. 30,77,78 Whether waterfowl (<i>Anatidae</i>) have a role in the dissemination of <i>Campylobacter</i> spp. that results in increased human disease is likely to be elucidated through development and greater use of typing methods. 79 Typing might allow links to be established between isolates of avian, environmental, and human origin. 79	Migrating ducks (<i>Anatidae</i>), passerine birds e.g. crows (<i>corvus</i>), pigeons (<i>Columbidae</i>) and seagulls (<i>Larus</i>), sparrows (<i>Passeridae</i>)	Europe, North America Asia
Helicobacter spp.	Enteritis (<i>Helicobacter canadensis</i>). 80,81 Possible transmission of <i>H. pylori</i> by contaminated water from feces of waterfowls (<i>Anatidae</i>)82	Geese (Anserinae), gulls (Larus), passerines (Passeriformes), terns (Sternidae), various wild birds	North America, Europe Australia
Other gram negative bacilli (<i>Pseudomonas</i> , <i>Aeromonas</i> , etc.)	Possible through faecal pollution of environmental water samples ^{72,83}	Geese (Anserinae), gulls (Larus)	Worldwide
Anaerobic bacteria	Possible through faecal pollution of environmental water samples e.g. gulls (<i>Larus</i>) ⁸⁴	Geese (Anserinae), seagulls (Larus), swans (Cygninae), wild ducks (Anatidae)	Worldwide
Anaplasmataceae Anaplasma phagocytophilum	Human granulocytic ehrlichiosis ^{85–87}	Passerine birds (<i>Passeriformes</i>) American Robins (<i>Turdus migratorius</i>), robins, songbirds (<i>Passeriformes</i>) veery (<i>Catharus fuscescens</i>), American warbler	North America, Europe Asia

Mycobacterium species M. tuberculosis	Tuberculosis. 88 Possible transmission of mycobacterium from humans to birds has been reported through close contact between humans and pet birds but it is not known if humans can acquire the infection from birds. 88	Green-winged macaw, psittacines (<i>Psittaciformes</i>) ^{88,89}	
Rickettsiaceae Coxiella burnetii	Possible through ticks ^{90,91}	Pigeons (Columbidae)	Europe, Asia
Vibrionaceae Vibrio cholerae	Cholera, non-cholera Vibrio infections ^{92,93}	Wild aquatic birds (Anatidae), gulls (Larus)	North America
(II) Viruses Bunyaviridae Nairoviruses: Crimean- Congo haemorrhagic fever (CCHF)	Possible transmission through ticks and transmission has been reported for other birds ^{94,95}	Crows (Corvidae), wild aquatic birds (Anatidae), passerines (Passeriformes), rooks, (Corvus frugilegus)	Europe, Asia, Africa
Coronaviridae Avian infectious bronchitis virus, other coronaviruses	Serological evidence in humans exposed to birds has been reported ⁹⁶	Passerines (Passeriformes), pheasants (Phasianidae)	Worldwide
Flaviviridae			Worldwide
Japanese encephalitis virus (JEV)	Yes ^{97–99}	Colonial ardeids (<i>Ardeidae</i>), herons (<i>Ardeidae</i>), marsh birds, quails (<i>Coturnix</i>)	
Other flaviviruses Murray Valley encephalitis virus (MVEV), Usutu virus (USUV)	Yes (MVEV) ^{100,101} NR (USUV)	Blackbirds (<i>Turdus merula</i>), wading birds, crows and magpies (<i>Corvidae</i>) (Usutu virus), Pelecaniformes (MVE virus)	
Sindbis virus	Ockelbo disease, 102,103 Pogosta disease, 104 plus possible transmission to humans as migratory birds are hosts of mosquitoes which are vectors for these viruses	Blackbird (<i>Turdus merula</i>), carrion crow (<i>Corvus corone</i>), passerine birds (<i>Passeriformes</i>) wild grouse (<i>Tetraonidae</i>), wild ducks (<i>Anatidae</i>)	
Tick-borne Encephalitis virus (TBE)	Possible through ticks ^{105–108}	Blackbirds (<i>Turdus merula</i>), sandpipers (<i>Scolopacidae</i>), wild mallards (<i>Anas platyrhynchos</i>), wild grouse (<i>Tetraonidae</i>), other wild birds	Europe, America
Herpesviridae Anatid herpesvirus 1, (duck plague virus), Marek virus	Marek's virus (transported by wild birds) has been associated with multiple sclerosis in humans. 109,110	Japanese quails (Coturnix coturnic japonica), passerines (Passeriformes), pigeons (Columbidae), raptors (North American raptors), wild anseriforms (Anatidae), geese (Anserinae), swans (Cygninae)	Europe, Asia, North America, and Africa
Paramyxoviridae Newcastle disease virus (NDV, avian parainfluenza virus 1, paramyxovirus-1)	Serological evidence in humans exposed to migratory birds has been reported. 96 Can cause self-limiting conjunctivitis as occupational exposure to affected poultry	Cormorants (<i>Phalacrocoracidae</i>), gulls (<i>Larus</i>), passerines (<i>Passeriformes</i>), pelicans (<i>Pelecanus</i>), raptors (North American raptors), waterfowls (<i>Anatidae</i>)	Worldwide
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Microorganism(s)	Potential for transmission to humans exists $(n = 50)$	Migratory bird species	Geographic area
Other Paramyxoviridae (pneumoviruses)	NR	Gulls (Larus), waterfowl (Anatidae)	Europe, Africa, Asia
Picornaviridae			
Egg drop syndrome virus	Possible through faecal pollution of environmental water samples with wildfowl droppings ^{111,112}	Coots (Fulica), grebes (Podicipedidae), herring gulls (Larus argentatus), migratory ducks (Anatidae), owls (Strigidae), storks (Ciconiidae), swans (Cygninae)	Worldwide
Foot-and-mouth disease virus	NR but according to some studies birds do not have an important role in the transmission of enteroviruses ¹¹³	House-sparrows (Passer domesticus), seagulls (Laridae), starlings (Sturnidae)	Europe
Reoviridae Avian rotavirus, orbivirus and other spp.	Not reported but evidence for transmission to mammals ^{111,114–116}	Wild geese (Anserinae), wild woodcocks (Scolopax)	Asia, Africa, Europe, America
Togaviridae Eastern (EEE) and Western (WEE) equine encephalitis viruses	Possible through mosquitoes that are vectors for these viruses 117,118	Cliff swallows (<i>Petrochelidon pyrrhonota</i>), finches (<i>Fringillidae</i>), American Robins (<i>Turdus migratorius</i> , smaller species of Passeriformes, several trans-Gulf	America
Venezuelan equine encephalitis virus (VEE)	Possible through mosquitoes that are vectors for these viruses ^{119,120}	migrant starlings (<i>Sturnidae</i>), waterbirds (<i>Anatidae</i>) Nestling birds such as Cliff swallows, North American shorebirds, songbirds (<i>Passeriformes</i>), wild ducks (<i>Anatidae</i>)	South to Central Americ
(III) Parasites			
Coccidia (Eimeria)	Possible through contamination with faecal material ¹²¹	Cranes (<i>Gruidae</i>), owls (<i>Strigidae</i>), wild pigeons (<i>Columbidae</i>), waterfowls (<i>Anatidae</i>)	North America, Asia, Africa
Cryptosporidium	Has been reported for other non-migratory birds ¹²²	Cranes (<i>Gruidae</i>), exotic seagulls (<i>Larus</i>), wild anseriforms: ducks (<i>Anatidae</i>), geese (<i>Anserinae</i>), swans (<i>Cygninae</i>) and wild birds (order <i>Passeriformes</i> , <i>Phasianidae</i> , <i>Fringillidae</i> , and <i>Icteridae</i>), waterfowl species (<i>Anatidae</i>)	America, Africa, Asia
Helminths parasites	Possible food-borne through eating small water fish. 123	Gulls (Larus), ducks (Anatidae), passerines (Passeriformes), waterfowl species (Anatidae)	Australia, Europe, Africa, Asia, America
	Cercarial dermatitis (swimmer's itch) due to exposure to marine schistosomes 124		
Sarcocystis	Possible through contaminated water ¹²⁵	Cowbirds (Molothrus), exotic birds, mallards (Anas platyrhynchos), passerines (Passeriformes), wading birds, wild anseriforms (Anatidae), geese (Anserinae), swans (Cygninae)	America, Africa, Europe

invertebrate vectors), others to the pathogen itself (e.g. stability of the agent in the environment), and lastly some factors relate to the environment (e.g. temperature, humidity). Studies of certain pathogens like influenza virus illustrate the interaction of factors that limit the transmission and subsequent establishment of an infection in a novel host species and may help us in understanding how and why some pathogens become capable of crossing host species barriers. ¹³²

Factors relating to the implicated pathogen and the affected species

Pathogens associated with wild and migratory birds may be transmitted to humans via several routes. Generation of contaminated aerosols by waterfowl flocks may result in respiratory infections through inhalation of dust or fine water droplets generated from infected bird feces or respiratory secretions in the environment (e.g. Newcastle Disease or chlamydiosis). 30 Birds can contaminate water with feces, nasal discharges, and respiratory secretions (e.g. influenza A virus, Enterobacteriaceae) resulting in a waterborne human infection after direct contact with aquatic environments. 30 Recently, the European CDC concluded that the bathing risk in the case of waters contaminated with the H5N1 virus cannot be excluded and should be assessed on a case by case basis even though the chance of such an event is highly unlikely. 133 Food-borne infections may result after consumption of infected carcasses of wild birds or raw or undercooked blood, organs, or meat, e.g., WNV, avian influenza A (H5N1), M. avium, Clostridium spp., Sarcocystis, Frenkelia. 52,63,134 Infections may lastly result after direct contact with the skin, feathers, external lesions or droppings of infected wild birds (e.g. avian pox, WNV encephalitis, H5N1, mycoplasmal conjunctivitis). A major source of wild bird-human contact is hunting and the cleaning of killed birds. Often birds are field-dressed by hunters with minimal protection bringing them in contact with blood, organs and feces. 30 Serologic evidence of avian influenza infection in hunters and wildlife professionals has been reported.⁵⁶ In addition, occupational exposure to avian species (e.g veterinarians) may increase risk of infections like avian influenza virus infection. Indirect infection may occur through the same routes if wild birds transmit the infection to domestic animals, e.g. poultry or via exposure to inanimate surfaces contaminated by bird secretions or droppings. Transfer of infected material can happen with shoes, clothing or other inanimate objects.

Wild birds when serving as reservoirs exhibit multiplication of the pathogen within their organism. Aggregations of bird species that occur during certain periods within the avian annual cycle may enable transmission of pathogens between individuals. Extreme examples for such aggregations can be found at moulting and staging areas of eared grebes *Podiceps nigricollis*, ^{135,136} at roosting sites for European starlings *Sturnus vulgaris*, at landbridges between continents (e.g. Gibraltar, Bosporus) widely used by soaring and gliding species like larger birds of prey and white storks *Ciconia ciconia* and at breeding sites of many seabirds. In terms of numbers, the vast amount of migratory birds do migrate solitarily in 'broad front' and therefore do not encounter an increased risk of pathogen transmission, while

some species travel hundreds to thousands of kilometres from their breeding grounds and re-fuel at distinct stopover sites. 137 These "staging areas" provide the opportunity for close intermingling of species that are otherwise widely separated during the major part of the year. 35,138 Thus, the theoretical opportunity for exchange of pathogens is increased among avian species, which make use of the same stopover sites. In such instances duration and concentration of the agent in the blood or the gastrointestinal tract of migrating birds are important for the subsequent infection of another competent vector that feeds or gets exposed in crowding situations or during stopover e.g. a tick. Several studies have recorded infections e.g. B. burgdorferi and human granulocytic ehrlichiosis (HGE) in ticks removed from birds. 36,37,87 Ticks commonly infest a wide range of avian species, especially, sparrows (Passeridae), thrushes and other ground foraging birds. 30,36,37,139,140 Although a wide range of tick species has been reported to parasitize wild birds, Ixodes spp. are the most likely ones to carry infections (e.g. B. burgdorferi) especially in Europe and North America. Ixodid ticks often attach to hosts for 24-48 hours while acquiring a blood meal. In tick-borne viruses, bacteria, and protozoa, the infectious larval or nymphal tick may remain attached to the body of a migratory bird for several days and then deposited during migration in a new geographic area. During migration, there is sufficient time for some birds to travel hundreds or even a few thousand miles before ticks complete feeding and drop off. Even if these birds have small tick burdens, their large numbers could result in substantial contributions to local tick populations in coastal areas. 40 There is even evidence of transhemispheric exchange of spirochete-infected ticks by seabirds indicating the capacity for wild birds to carry infected ticks for long distances. 141 Moreover, birds can carry infections in their bloodstream which is introduced to local population of ticks at other sites. Therefore, birds play an important role not only in maintaining infections such as B. burgdorferi sensu lato in areas of endemicity, in addition some of them, through their migration, also play a role by spreading ticks within and between continents. 36,139,142,143

Exposure to tick-borne diseases is primarily peridomestic. so the contribution to tick related human infection of avian ticks relative to mammalian ticks around dwellings is critical. 38 Birds that are implicated in peridomestic transmission of tick related infections to humans, especially in North America, include American robins (Turdus migratorius), northern cardinals (Cardinalis cardinalis), and song sparrows (Melospiza melodia) that frequently use backyard environments and some of which are commonly seen at bird feeders. Therefore, they are likely to drop engorged larvae in peridomestic environments like lawns and gardens, 40 where ticks are less common than in woods and at wood edges but more likely to encounter people. 38,144 Even though the survival of nymphs is low in open habitats, the contribution of birds to human infection in the peridomestic environment could be substantial and deserves further study. 40

An additional factor is the physiologic stress that wild migratory birds suffer with migration, a risk factor for immunosuppression and increased susceptibility to infectious diseases. Avian species may exhibit an increased susceptibility to certain pathogens (e.g. *West Nile virus*) compared to other vertebrate groups.^{3,4} Changes and

adaptations occur in migratory birds during long-distance migration. ⁶³ For some birds, the stress of migration can lead to reactivation of otherwise latent infections. ¹⁴⁵ West Nile virus was isolated from migrating birds that were under migratory stress. ¹⁴⁶ However, an opposing argument is that infected migratory birds could not survive long-distance travel; thus their role in transmitting communicable diseases is of less importance. ¹⁴⁷ For example, in the case of avian influenza most outbreaks in wild birds seem to reflect local acquisition of infection from a contaminated source, followed by rapid death nearby. ¹⁴⁸ There is only limited evidence that some wild birds can carry the virus asymptomatically, and no evidence from wild bird outbreaks that they have done so over long distances during seasonal migration. ¹⁴⁸

Understanding the balance between the changes and adaptations that occur in migratory birds during long-distance migration is important to comprehend susceptibility of certain migratory birds to develop infections. Similar factors e.g. age and bird gender may in addition influence migratory patterns leading to spread of diseases in novel geographical areas.³

Factors relating to the implicated pathogen and the environment

Migrants of most bird species in the New World seldom use the same stopover sites on northward, spring migration as they do on southward, fall migration. This is because migration routes are determined by complex interactions of environmental factors such as direction of prevailing winds, weather patterns, location of available food resources and geographical barriers (e.g. large bodies of water, deserts and mountains). These factors seldom combine to favour the same route in different seasons.3 Seasonality is a significant factor influencing both, wild birds (wild resident and migratory species) and other vectors e.g. mosquitoes, ticks leading to changes in transmission dynamics. 149-151 For mosquitoes, a spring population peak in Europe and North America occurs during the spring migration of birds. 146-148 The effect of seasonality in the flyway patterns of major migratory birds was observed for certain diseases such as West Nile virus encephalitis. The incidence of West Nile virus disease is seasonal in the temperate zones of North America, Europe, and the Mediterranean Basin, with peak activity from July through October. 152 Both avian and human infection rates drop to near zero as winter approaches and mosquitoes become dormant. 153 Season is important for some non-vector-borne pathogens, as well. For example, influenza A viruses remain infectious in water at lower ambient temperatures and at the same time major congregations of migratory waterfowl occur, increasing the likelihood of transmission among birds. Furthermore, numerous bird species (e.g. crows and gulls) are attracted to untreated sewage, garbage dumps, manure, and other sources of enteric pathogens that can then be transmitted to humans. These areas should be appropriately covered and not open to the access of wild migratory birds.

Migratory bird flyways and transmission

Long-distance migration is one of the most demanding activities in the animal world and several studies demonstrate

that such prolonged, intense exercise leads to immunosuppression exacerbating the possibility of spreading infections. On the other hand, infected symptomatic wild birds may act as vectors over shorter distances. 154 Understanding bird migration, avian migration patterns and infectious diseases of birds would be useful in helping to predict future outbreaks of infections due to emerging zoonotic pathogens and can provide important information that could explain the pattern of spread of certain infectious agents. Numerous variations in flyways exist. For some ocean migratory wild birds, a nomadic wandering that can appear random is probably related to poorly understood weather or ocean conditions. 155,156 Major migratory flyways, especially between continents are known to be used by migratory birds when commuting between breeding and wintering areas and vice versa. Nevertheless, these flyways are only used by a fraction of the existing species on the move, predominately by waterfowl and soaring and gliding migrants like large raptors and storks which aggregate and follow fairly easily defined routes.

The complex overlapping of major flyways and the lack of information on migratory species potentially involved in the spread of disease make simple association of wild migratory flyways with outbreaks of certain infections extremely difficult despite the significant amount of literature on the subject. For example, in Alaska, there is a notable overlap between the Pacific and East Asia/ Australasia flyways through which scientists believe avianflu-infected migrating birds, such as the bar-tailed godwit (Limosa lapponica), dunlin (Calidris alpina), and red knot (Calidris canutus), will transfer the Asian strains of H5N1 influenza virus to North American birds over the next few months¹⁴ although this was not confirmed in a recent study. 157 On the other hand, other more local migratory bird routes have been described in association with West Nile virus outbreaks.3

Societal factors

Furthermore, societal factors like captivation of wild birds in zoos and importation and sale of wild birds as pets should also be considered as important factors which can enhance the spread of pathogens from wild birds to humans. *Cryptosporidium* has been reported to be transmitted from some non-migratory birds in zoos to humans. ¹²² A theoretical similar risk for *avian influenza* exists as *avian influenza* was recently isolated from a wild swan in the Dresden zoo in Germany. ¹⁵⁷ Similar risk can be encountered in bird parks since outbreaks of infections related to birds like psittacosis have occurred. ¹⁷ Finally, the international trade of exotic pet birds carrying influenza A viruses enhances the risk of worldwide dissemination of potentially virulent influenza A virus and may pose a serious health threat to humans. ¹⁵⁸

Limitations of the current literature review

There are several limitations of this work and clearly further work is necessary. Some of the identified agents are quite ubiquitous in the environment raising the question about how to quantify the additional impact wild resident

and migratory birds may have on transmission. There is still scientific debate over the actual role migratory birds might play in the transmission of certain communicable diseases. In support of this argument we did not find any evidence for direct transmission from wild and migratory birds to humans for any of the identified pathogens the only exception being the cluster of H5N1 human cases in Azerbaijan. 16 In addition, in many cases, there was no further available information that would allow further elucidation of the real epidemiological role played by wild birds in the ecology of the considered infections, especially in underdeveloped countries. Many reports do not exactly clarify how the birds are implicated in the transmission of these infections and in the majority of cases this transmission could not be established by adequate scientific methods. Thus, in many of the reports reviewed herein, there were no data regarding serologic assays or molecular diagnostic techniques used to detect and characterize pathogens and identify birds as vectors of disease. In these cases only associations of these infections with migratory birds could be made (Table 2).

The evidence reviewed herein suggests that many pathogens can infect multiple host bird species and that these pathogens in theory could be responsible for emerging infectious disease outbreaks in humans and wildlife. However, the ecologic and evolutionary factors that constrain or facilitate such emergences are poorly understood. In the literature, a different terminology is used to describe the interaction between hosts, including wild birds, and pathogens. Terms such as multihost pathogens, reservoir hosts, and spill-overs are frequently used, but often such different terms are used to describe the same phenomenon. There is a need for a single, standardised comprehensive framework that characterizes disease outcomes based on biologically meaningful processes. An example of such conceptual framework is based on the pathogen's betweenand within-species transmission rates and can be used to describe possible configurations of a multihost-pathogen community. 159 In particular, the much-overused terms reservoir and spill-over can be seen to have explicit definitions, depending on whether the pathogen can be sustained within the target host population. 159 However, the paucity of available published data did not allow us to determine whether the involved species of certain wild birds serve as reservoir or spill-over. Finally, only few studies have reviewed the role of migratory birds in transmission of all different infections and these studies remain descriptive. 112

Migratory birds cannot be blamed for recurrent outbreaks at the same geographical location over subsequent years unless there is in an introduction of the pathogen to known or novel avian or other animal reservoir hosts and vectors. Furthermore, for some viruses that are considered to be transmitted by wild migratory birds (e.g. West Nile virus), duration of high levels of viremia for most species tested has been found to be limited and usually less than 24 hours. However, exceptions to that rule exist. The house sparrow (Passer domesticus) has demonstrated WNV viremia of sufficient duration to indicate its ability to serve as a competent host for WNV.³

Furthermore, other modes of transmission such as the import of infected products may be of equal importance in

the spread of diseases like avian influenza and scientists are still debating the evidence of the role of migratory birds in the wide geographical spread of the influenza A (H5N1) virus. Highly pathogenic avian influenza viruses have been isolated rarely from wild birds and, apart from a single case in common terns in South Africa, 160 when they have, it has usually been in the vicinity of outbreaks of highly pathogenic avian influenza virus in poultry or geographically and chronologically close to known outbreaks in poultry. In fact the de novo generation of highly pathogenic avian influenza virus strains (restricted to subtypes H5 and H7) so far has been described to have occurred only in domestic poultry and the occurrence of highly pathogenic avian Influenza viruses in wild birds is most likely the result from spill-overs from the poultry population.

Another important limitation is that there is no way to predict whether the comprehensive lists presented in this paper may expand in the near future. Moreover, the fact that a lot of the pathogens carried by wild and migratory birds that are presented in Table 2 have not been associated with human infection does not mean that these pathogens cannot cause human infection through routes presented for other pathogens in the same table.

Future directions

Identifying links between environmental factors and infectious disease risk is essential to understanding how human-induced environmental changes will affect the dynamics of human and wildlife diseases. Studying large wetland areas, and by extension, intact wetland bird communities, may represent a valuable ecosystem-based approach for controlling infections caused by migratory birds including WNV. 161 Recent evaluations suggesting links between high biodiversity among wild birds and reduced vector-borne disease risk, such as WNV, may lead to a better understanding of distribution patterns of such diseases.⁴⁸ Recent findings on the origin of the WNV infections suggest a single species to act as a super spreader and the transmission of WNV appears in new light. 162 These recent findings demonstrate imposingly how important detailed studies on contact rates between vectors and host species are and how careful interpretations need to be made before drawing any conclusions. Estimation of the infection rate of wild bird populations with human pathogens or with other vectors carrying pathogens is clearly an indicated future challenge required to judge the possibilities of bird to human transmission of pathogens. The same accounts for the transmission between and within bird species. Recent investigations indicate the influence of social and sexual behaviours and their seasonal components on intra-specific transmission, 163,164 while the inter-specific transmission rate remains speculative. Birds are considered to show behavioural changes due to pathogen infection, which will considerably influence transmission rates. 163 Furthermore, accurate data on the speed and direction of migratory birds may enable us to predict the timing of bird migration in more detail; this will assist in monitoring the risk of infections that may be caused by wild birds. While this knowledge is available for larger bird species due to the use of satellite tracking, only limited data are available on the

individual level for some North American songbirds with the use of radio-telemetry tracking. ¹⁶⁵ Producing maps depicting the ecology of the vectors including mosquitoes and ticks ecology in combination with maps of migratory routes of wild birds along with access to real time climatic data could be the key for developing a real time early warning system for forecasting vector-borne disease outbreaks. ¹⁶⁶

The spatial and temporal pattern of migration of wild birds as well the spatial distribution throughout the annual cycle can provide further insight. Application of stable isotope analysis has already resulted in new insights where bird populations spend the time between the seasonally reoccurring breeding events, ¹⁶⁷ a knowledge which can be of great importance for future predictability of disease outbreaks.

Human medicine often does not delve deeply into the role of animals in the transmission of zoonotic agents and veterinary medicine does not cover the clinical aspects of human disease. However, to effectively and completely cover the area of infections associated with wild birds would require involvement of both physicians and veterinarians especially those dealing with avian species. 168 Unfortunately, one recent study demonstrated that communication between physicians and veterinarians about zoonotic diseases is largely absent. 168 Therefore, one important factor that could potentially explain the paucity of available data regarding the transmission of pathogens from wild birds to humans could be the lack of communication between physicians and ornithologists. To most effectively decrease the risk of infections associated with wild birds, the public health and animal health sectors must collaborate in developing strategies to decrease human exposure to pathogens carried by wild birds.

An effective public educational campaign could also put in perspective and clarify myths and realities about the risk of acquiring infections associated with wild birds. Activities near geographical areas with extensive wild bird activity really carry minimal risk especially if people take personal protective measures for high risk activities such as handling dead wild waterfowl. Normal behaviour that complies with general hygienic standards should suffice.

Conclusions

We attempted to summarize the published scientific evidence regarding the direct and indirect roles of wild birds in transmission of certain infections to humans. Although we could not fully define this role and it appears that further research is necessary, several conclusions can be made. First, there is no real evidence for direct wild bird-human transmission besides rare examples occurring under exceptional circumstances. Several human infections can theoretically be transmitted from wild and migratory birds although the scientific base for most of the associations remains speculative. These findings are expected for zoonoses, which usually require the amplification in an animal species cycle before spill-over to humans. Wild and migrant birds are most important in seeding pathogens into these amplification systems. This explains why most of the association with transmission from bird to human may only occur indirectly. On the other hand, there is strong

evidence for the dispersal of pathogens to new geographical locations by migrating birds but it is largely unknown how this will affect transmission to humans. The recent emergence of infections like West Nile virus and influenza A in various parts of the world is a prominent example of how rapidly and widely a migratory bird associated disease can spread. The potential factors and mechanisms involved in the transmission of such infectious agents from birds to humans need further elucidation. An in-depth comprehension of avian migration routes as well as further research using advanced molecular testing of the prevalence, pathogenesis, and clinical associations of several pathogens that are transmitted to humans from the various migratory bird species would lead to a better understanding of the transmission dynamics of diseases carried by avian species helping to predict future outbreaks of relevant human infections.

Conflict of interest

None.

Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.jinf.2007. 11.001.

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