

Review

# The Ecology of Emerging Infectious Diseases in Migratory Birds: An Assessment of the Role of Climate Change and Priorities for Future Research

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**Abstract:** Pathogens that are maintained by wild birds occasionally jump to human hosts, causing considerable loss of life and disruption to global commerce. Preliminary evidence suggests that climate change and human movements and commerce may have played a role in recent range expansions of avian pathogens. Since the magnitude of climate change in the coming decades is predicted to exceed climatic changes in the recent past, there is an urgent need to determine the extent to which climate change may drive the spread of disease by avian migrants. In this review, we recommend actions intended to mitigate the impact of emergent pathogens of migratory birds on biodiversity and public health. Increased surveillance that builds upon existing bird banding networks is required to conclusively establish a link between climate and avian pathogens and to prevent pathogens with migratory bird reservoirs from spilling over to humans.

**Keywords:** influenza A virus, malaria, salmonella, West Nile virus, zoonoses

## ANTHROPOGENIC DRIVERS OF DISEASE TRANSMISSION BY MIGRATORY BIRDS

Billions of birds migrate between continents annually and have been doing so for millions of years (Moreau and

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Monk 1972; Alerstam 1990; Newton 2008). As a consequence, with the exception of remote oceanic islands, avian pathogens have had ample opportunity to spread globally. For example, since avian *Plasmodium* (malaria) parasites first evolved, possibly as recently as nine million years ago (Ricklefs and Outlaw 2010), birds have dispersed these pathogens around the world via migratory flyways. To the extent that long-distance movements by infected hosts can lead to the global spread of a pathogen (Rvachev and Longini 1985), one might expect avian parasites to be

uniformly mixed, and annual changes in pathogen exposure in a particular host population to be small. In fact, however, most avian parasites including malaria exhibit considerable spatial variation (Bensch and Akesson 2003; Fallon et al. 2005). Furthermore, preliminary evidence suggests possible range expansions and increases in virulence of pathogens with migratory bird reservoirs. A noteworthy example is West Nile virus (WNV), which has spread over southern Europe and North America in the last 15 years and has evolved novel strains with increased pathogenicity in avian and mammalian hosts (Kilpatrick 2011; Ulbert 2011).

Although land conversion and anthropogenic introduction of non-native host species caused many emergent avian diseases in the past, such as avian malaria in Hawaii (Van Riper III et al. 1986), recent outbreaks of avian diseases may be arising as a consequence of climate change. Numerous pathogens of migratory birds, including aspergillosis, avian botulism, avian cholera, avian influenza, avian malaria, and Newcastle disease virus are expected to increase their geographic distributions as result of climate change (for details, see Gilbert et al. 2008; Atkinson and LaPointe 2009; Traill et al. 2009). For example, the spread of tick-borne encephalitis (TBE) virus to higher altitudes in the Czech Republic (Danielova et al. 2010) has been related to the effect of increasing temperatures on the distribution of avian hosts that spread ticks carrying the TBE virus. Preliminary evidence suggests that climate affects the spread of H5N1 by waterfowl in Europe to the extent that harsh winters limit the movement of migratory ducks, crowding them into smaller areas and creating conditions conducive to H5N1 transmission (Keller et al. 2009; Reperant et al. 2010), though more ecological studies of this phenomenon are needed (Globig et al. 2009). Furthermore, climate change is increasing precipitation in eastern North America, which can lead to an expansion of wetlands and greater abundance of migratory ducks, which are influenza reservoirs (Vandegrift et al. 2010).

The principal causes of emerging infectious diseases (EIDs) in humans since 1940 include farm size, international migration and travel, and land use change (Jones et al. 2008). The intensification of agriculture on large farms explains 13% of EIDs whereas land cover change explains 18%, and international travel and migration and related factors account for a further 26% (Keesing et al. 2010). The H1N1 pandemic of 2009 illustrates the importance of international travel for pathogen spread insofar as H1N1 arrived earlier in countries with high numbers of

international flights from Mexico, where the virus is hypothesized to have originated (Hosseini et al. 2010). The pet trade (Reed et al. 2004) and exotic species introductions (Atkinson and LaPointe 2009) have also contributed to the spread of EIDs, though their contributions have not been systematically analyzed. Thus, the spread of pathogens by migratory birds may be linked to the interaction of climate change, avian migration, and human movement and commerce. In the near term, climate change has the potential to destabilize coevolved host-pathogen interactions, for instance, by increasing the rate of parasite development and altering the seasonality of transmission as in nematode parasitism of the Red Grouse in Scotland (Cattadori et al. 2005; Brooks and Hoberg 2007). Global warming could provide conditions for tropical parasites to spread towards higher latitudes along with their vectors or improved transmission conditions (Garamszegi 2011). Some range shifts will result in novel and evolutionarily untested host-pathogen interactions, which could cause host shifts, potentially creating an EID. Understanding the causes of EIDs has tremendous value measured in human lives saved and economic losses avoided through prediction, prevention, and mitigation (for example, the cost of introduced diseases is \$41 billion per year in the US alone (Daszak et al. 2000)). This raises the question of what policies might be effective for controlling emergent avian pathogens.

This review complements several recent studies on climate change, wild birds, and emerging diseases (Salomon and Webster 2009; Faaborg et al. 2010; Jiguet et al. 2010; Slenning 2010; Vandegrift et al. 2010; Altizer et al. 2011; Saino et al. 2011). Our review is unique in that we focus on the spillover of pathogens from wild birds to humans and we assess the benefits and feasibility of policies for monitoring emergent avian pathogens and ultimately preventing their spillover to humans and livestock, such as sampling systems built upon bird banding networks and biobanks to store pathogens collected from wild birds.

## LEVERAGING RESEARCH FOR PATHOGEN CONTROL

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The control of EIDs that may appear as a result of climate change will require an interdisciplinary approach. Infectious diseases of birds, defined here as the invasion of an avian host by microorganisms followed by growth of the microorganisms that trigger clinical symptoms in the host

(Kayser et al. 2005), have traditionally been studied by medical and veterinarian scientists. On the other hand, ecologists have focused on other types of species interactions, including predator–prey systems. Birds harbor innumerable species of pathogens, few of which are well known (Supplementary Text 1 reviews well-studied avian pathogens).

Recent advances in pathogen screening and host tracking illustrate how collaborations across disciplines lead to rapid progress. Techniques for testing and typing pathogens are becoming increasingly sophisticated and fast as new molecular and serological methods and genomic resources develop. Interdisciplinary collaborations could improve the detection of emerging pathogens of avian migrants. For example, ecologists have expertise in the monitoring of wild birds at banding stations or rehabilitation centers (Berthold 2001), whereas virologists have expertise in the detection of novel avian pathogens using methods such as microarrays (Kistler et al. 2008). A migratory bird-monitoring network operated by experts from these two fields could result in earlier detection of emerging avian viruses. Recent progress in the screening of avian pathogens has been accompanied by advances in the tracking of their hosts. Knowledge of bird dispersal and migratory connectivity, defined as the use of the same breeding and wintering areas (Webster et al. 2002), are accumulating at an unprecedented rate as a result of advances in tracking devices (satellite transmitters (Tomkiewicz et al. 2010) and geolocators (Stutchbury et al. 2009)) and population assignments based on stable isotopes (Hobson and Wassenaar 2008) and genetic markers such as microsatellites and single nucleotide polymorphisms (SNPs) (Novembre et al. 2008). In this review, we outline the concerted research actions required for monitoring avian pathogens to document host shifts and predict EIDs. Advances in our understanding of connectivity can increase the tractability of monitoring by identifying where birds winter and breed, which can inform the design of surveillance programs. We hope to recommend actions that can ameliorate the impact that emergent pathogens may have on biodiversity and public health. Furthermore, we note that analyzing avian pathogens that are not serious health concerns for humans or livestock may nevertheless provide important insights about disease ecology and evolution. For example, malaria parasites are the most well-studied avian pathogens and could be used to test hypotheses about host shifts that lead to EIDs and pathogen range expansions in response to global climate change.

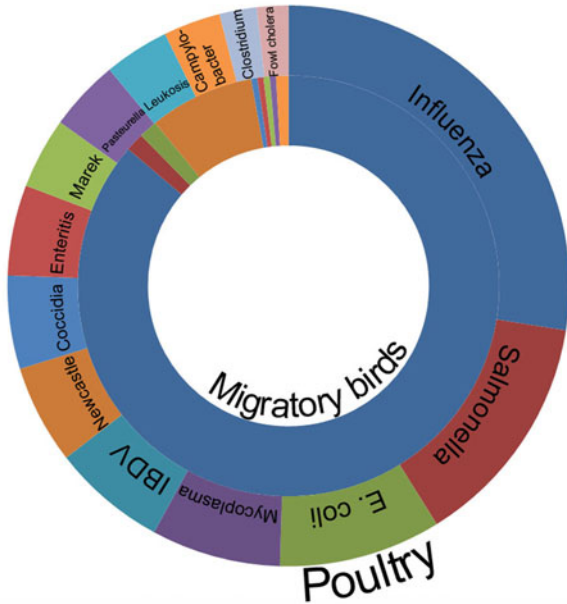
Investigating these questions using avian malaria as a model organism may be more straightforward than clinical studies of humans.

## GAPS IN OUR KNOWLEDGE ABOUT THE TRANSMISSION OF PATHOGENS BY MIGRATORY BIRDS

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The ecology and evolution of pathogen dynamics are so complex that anticipating the emergence of particular diseases is only a distant goal. Indeed, we still do not fully understand why ordinary diseases sometimes develop into EIDs (Jones et al. 2008). Past experience provides some insight into key elements of the biology of pathogens and their hosts that could help in developing effective prophylaxis, preventing spread, and ameliorating impacts of EIDs (Jones et al. 2008; Parrish et al. 2008). There has been a research bias in favor of domestic birds with 60 times as many papers published on infectious diseases of poultry than those of migratory birds; furthermore, almost all of the pathogens that have been studied in wild birds are those that also affect poultry (Fig. 1). Poultry studies have also examined a much more diverse set of pathogens. More than two dozen different pathogens account for 70% of poultry publications whereas Newcastle disease virus and influenza A virus comprise 70% of publications about pathogens of migratory birds. In particular, 64% of studies on infectious diseases of migratory birds have examined influenza A whereas only 18% of poultry studies have dealt with this virus (Fig. 1). Thus, there is an opportunity to gain a more comprehensive understanding of wild bird diseases by examining a more diverse set of pathogens. The analysis of a broader range of diseases of wild birds could provide valuable data that could be used to test the hypothesis that parasites with a broad host range of hosts are more likely to switch hosts, triggering an EID (Woolhouse and Gowtage-Sequeria 2005).

To provide a plan to guide practical efforts in EID research, we define some of the open questions related to migratory birds, climate change, and disease, and assess their difficulty and the ramifications of answering them. We recommend that research efforts focus initially on lower difficulty, higher importance questions (Table 1). For example, an important question is how the geographic ranges of migratory birds and insect vectors may shift under climate change. This question is lower difficulty because it can potentially be resolved through the use of



**Figure 1.** Research on poultry diseases has examined a greater diversity of pathogens than studies of migratory birds. The *outer disc* represents publications retrieved from PubMed with the medical subject headings major topic “poultry disease” ( $n = 17,742$ ). The *inner disc* represents articles retrieved using the major topics “bird diseases” (excluding poultry, pets, and zoo animals, and non-migratory wild birds) ( $n = 284$ ). Each *color* represents one pathogen. The width of the *colored segment* of the disc is proportional to the fraction of studies focused on the pathogen. *IBDV* infectious bursal disease virus.

species distribution and physiological models (Kearney and Porter 2009). Furthermore, improving the resolution of connectivity between breeding and wintering areas is important because it can define demographic units within migratory bird species, which can shed light on which units are important for maintaining pathogens. This question is lower difficulty because it can be resolved through the development of SNPs that are informative and differentiated across the extremes of the range of migratory bird hosts as well as through the combination of genetic and

isotopic data (Novembre et al. 2008). On the other hand, predicting host shifts that generate EIDs is of paramount importance but remains challenging due to the difficulty of identify adaptive mutations and linking them to human activities (Pepin et al. 2010). Lastly, determining whether the disease environment is worse in the Tropics for avian migrants is important but difficult because there have been relatively few in depth community studies in the tropics. Better coordination among sampling campaigns and increased funding to analyze and archive samples could ameliorate this.

### CONSEQUENCES OF KNOWLEDGE GAPS

Because birds carry pathogens that can impact humans and livestock, understanding the roles of birds in the transmission pathways of these pathogens would be a great benefit to disease management. This understanding will depend on basic knowledge of bird pathogen distributions, combined with data on migration pathways and connectivity of bird populations (Supplementary Material, Section 2).

Endemic and threatened bird species risk contracting novel pathogens that might cause further decline and possibly extinction. Galapagos penguins (*Spheniscus mendiculus*) have recently been found to be infected by *Plasmodium* parasites, not previously encountered in any birds on the Galapagos (Levin et al. 2009). Migratory birds appear to be an important mechanism for the introduction of pathogens to the Galapagos (Kilpatrick et al. 2006a) and their role in the spread of avian malaria to these islands merits further study. If this is a novel and virulent parasite to penguins, it adds a new threat to this endemic population presently numbering only 1,500 birds. Moreover, spread to other endemic birds on the Galapagos might challenge the entire avian community. The *Plasmodium* lineages found in Galapagos penguins have previously not

**Table 1.** Open questions of high importance related to migratory birds, climate change, and disease, organized by difficulty

How will distributions of competent and naïve migratory bird hosts shift under climate change?	How often are host shifts that produce EIDs caused by anthropogenic habitat disturbance in overwintering and breeding grounds?
Can the resolution of connectivity between breeding and wintering areas be improved to define demographic units with respect to pathogens?	Is the disease environment for avian migrants worse in tropical resting areas or in temperate breeding areas?
Low	High
	Difficulty

been reported from any other bird species (Bensch et al. 2009b), and might therefore represent an endemic, and until now overlooked, parasite of the Galapagos penguin, and not an EID. However, because our knowledge of the geographic and host distribution of avian *Plasmodium* parasites is incomplete, this one might recently have been introduced. Hence, this penguin *Plasmodium* and its potential spread on the Galapagos warrant close surveillance.

Many national and international programs designed to monitor biodiversity and environmental quality are based on long-term censuses of common bird species. In order to relate such population trends to changes of land use, methods of agriculture and forestry, global warming, and invasive species, we must understand the extent to which these changes might be driven by pathogens. Without monitoring pathogens, we will fail to recognize all but those that cause frequent deaths and apparent lesions, as in the recent UK outbreak of *Trichomonas gallinae* in finches (Robinson et al. 2010). Furthermore, only monitoring common birds may be insufficient to predict the spread of pathogens by avian hosts to the extent that relatively uncommon species may be super-spreaders that infect a large number of individuals, as is the case with the transmission of WNV by American Robins (*Turdus migratorius*) (Kilpatrick et al. 2006b, 2010). Disease outbreaks can also have cascading effects beyond the species most affected by the pathogen. The outbreak of *Mycoplasma gallisepticum* in eastern North America in the mid-1990s reduced the population of house finches by 50% (Hochachka and Dhondt 2000). However, the decline of the house finch has been paralleled by an increase of house sparrows, supposedly resulting from reduced interspecific competition (Cooper et al. 2007). Moreover, host species diversity may itself help to predict the spread of EIDs. For example, the incidence of WNV in humans was lower in areas with greater richness of wild birds (Swaddle and Calos 2008).

## WHY NOW?

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This is a critical time to study the interrelation between migration and disease. The temporal and spatial dynamics of both pathogen and avian hosts are expected to change dramatically as a result of climate warming. Mistiming between spring arrival dates and peak food in northern latitudes is already well documented and in some cases has resulted in declines of some migratory bird populations (Both et al. 2006). Timing is also an important determinant

of disease exposure when pathogens spread from resident birds to migrants. For example, in Egypt, the prevalence of H5N1 in resident birds is highest in early spring, but most migratory birds currently arrive in late spring (Abdelwhab et al. 2010). However, if migrants arrive earlier in the spring due to climate change, their exposure to H5N1 could increase substantially.

Geographic ranges of many temperate and tropical species are changing, which could bring potential pathogens and hosts into contact for the first time. A study of over 250 species in North America revealed that species are shifting northward at rates as high as 1.5 km per year (La Sorte and Thompson 2007). Bird species' ranges are also moving north in Europe (Devictor et al. 2008). Although climate warming will likely shift the geographic ranges of infectious diseases, these changes probably will not result in a net increase in area occupied. Nonetheless, warming will likely bring hosts into contact with new pathogens for the first time, a first step in the emergence of any new infectious disease. Such novel contact is of increasing concern for EIDs affecting humans, although correlations with temperature will likely be complex, as in the case of the relationship between temperature, viral genetics, and vector competence in WNV (Kilpatrick et al. 2008).

It is important to note that patterns of connectivity in migrant birds are not necessarily the same as the connectivity of their parasites. The ability of migratory birds to spread pathogens between continents will depend on the duration of infection; for instance, individual waterfowl can spread H5N1 up to 2,900 km during the period when the infection is asymptomatic (Gaidet et al. 2010) and the virus might be spread even further through relay transmission by successively infected individuals. In comparison to the African-European system, in which 186 migratory species winter in sub-Saharan Africa with an area of 21 million km<sup>2</sup>, the available habitat in the North American-Caribbean system is more concentrated (250 migratory species winter primarily in just 2.7 million km<sup>2</sup>), resulting in a higher density of migrants and conditions more conducive to disease transmission (Newton 2008).

Genetic and isotopic analyses of a single feather can now be used to track where an individual was born and where it molted its feathers, providing a means of establishing patterns of migratory connectivity (Smith et al. 2005; Hobson 2011; Irwin et al. 2011). These approaches require genetic data from bird specimens as well as information about molting, winter quarters, and food sources. Unlike extrinsic tracking devices such as radio transmitters

and bird bands, genetic and isotopic markers can also help identify the appropriate spatial scales for understanding population trends—a problem that has hindered spatial analysis of trend data (Chamberlain et al. 2000; Bensch et al. 2009a; Rolshausen et al. 2010). Combining genetic and isotopic data has proved effective for assigning avian migrants to source populations (Kelly et al. 2005). Extrinsic tracking devices have also improved (Stutchbury et al. 2009; Tomkiewicz et al. 2010). Satellite transmitters have become smaller and lighter; data loggers weighing less than a gram can be attached to small passerines and used to track individuals across their annual cycle. Furthermore, movement modeling can be combined with the screening of wild birds for pathogens to predict geographic hotspots of avian viruses (Fuller et al. 2010).

## HOW ARE PATHOGENS INTRODUCED AND MAINTAINED IN MIGRATORY BIRD POPULATIONS?

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Mechanisms that account for how pathogens persist in avian migrants can be classified into those acting during non-migratory periods (breeding, pre-migration staging, and wintering) and those at work during migration. Regarding the non-migratory period, one behavior that can explain the spread of an infectious agent in ducks is pair formation, in which males follow females to breeding areas that may be far from the males' natal sites, providing pathogens an opportunity to colonize new breeding populations (Alerstam 1990). Crowding at breeding or molting locations also facilitates disease transmission. For example, in lakes in northwest China, the prevalence of H5N1 increases with the density of breeding birds (Li et al. 2010). The spread of an infection may depend on direct bird-to-bird transmission as well as transmission from an environmental source. For instance, coupled models of environmental and direct transmission provide the best fit to observed cycles of AIV in North American and European waterfowl (Breban et al. 2009; Roche et al. 2009).

During the migratory period, factors contributing to disease spread include weakening of the immune system due to the stress of migration, which can trigger latent infections or increase susceptibility to new ones (Altizer et al. 2011). Additionally, in comparison with resident birds, avian migrants are exposed to a greater range of vectors and pathogens as they travel through new areas (Newton 2008). For instance, migrants can acquire infections en route via the

spillover of pathogens from heterospecifics such as poultry. Furthermore, infected individuals of the same species may intermingle at feeding or stopover areas during migration, enabling viruses that infect these birds to exchange gene segments.

## STRATEGIES FOR THE FUTURE

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Experience has provided certain generalizations concerning EIDs, for example that they are often associated with host species introductions to new regions, with practices such as feedlots and garbage dumps that concentrate populations of potential disease carriers, or with increased contact of humans or livestock with wildlife following habitat conversion to agriculture or urbanization. These patterns underscore the importance of a “One Health” approach that recognizes that emerging diseases arise from the convergence of the human, animal, and environmental domains (King et al. 2008) and we believe that understanding the consequences of pathogen spread by birds will benefit from efforts of interdisciplinary research groups. Furthermore, these generalizations suggest that targeted screening of known pathogens, or close relatives, in wildlife populations would provide an improved picture of the risks of habitat alteration or of certain source areas for invasive species. For example, such screening has recently discovered that gorillas are reservoirs for the human malaria pathogen *Plasmodium falciparum* (Liu et al. 2010), which would indicate the value of additional research on other primates and on potential vectors of the disease. The finding that bats in Madagascar are infected with a *Hepato-cystis*-like pathogen most closely related to avian hemsporidians (Duval et al. 2007), emphasizes the possibility of the spread of EIDs across large taxonomic distances, suggesting that broad screening of potential pathogen reservoirs is necessary.

While comprehensive local screening is practical only on limited geographic scales, it would be possible in some cases to make use of ongoing programs, such as the nearly global effort in banding birds as a way of monitoring population changes. Monitoring in wintering areas of migrants is particularly important, especially where wintering migrants are in contact with domesticated animals and dense human populations. With minimal training and supplies, bird banders could provide blood and other samples to central labs, which would process the materials and assemble data on the geographic and taxonomic

distribution of pathogens of interest. Such an effort would require a long-term commitment of substantial funding, but it would provide currently unavailable knowledge of the dynamics of pathogens in natural populations of hosts, which might lead to a better understanding of the emergence of epidemics within natural host populations. Long-term storage of samples would allow comparisons of pathogen distribution and abundance over decadal periods. The US National Science Foundation is supporting a National Ecological Observatory Network, whose development is estimated to cost close to US\$ 400 million, with an estimated annual budget of US\$ 100 million. A more modest expenditure would support the beginnings of a network to observe large-scale changes in the distribution and abundance of selected pathogens. We estimate that such a network could collect and screen 10,000 samples from migratory birds in North and Central America for \$2 million/year. The costs associated with the spillover of avian pathogens to humans and poultry, the world's number one protein source are astronomical; for example, the next influenza pandemic could cost \$71.3 billion in the US alone and \$330 billion globally and result 1.4 million deaths (Meltzer et al. 1999; McKibbin and Sidorenki 2006). In light of this, the US Agency for International Development (through programs such as PREDICT), Australia's AID, and the EU have each invested more than \$150 million in international initiatives for the surveillance and control of avian influenza and other emerging pathogens (Keusch et al. 2009). It is our view that including migratory bird surveillance in these types of initiatives has the potential to yield substantial economic and public health benefits by contributing to a reduction in the spillover of wild bird pathogens to humans and livestock.

## SUMMARY

Pathogens carried by wild birds such as flu and salmonella significantly impact the poultry industry and human health. Fuller et al. reviewed the literature on infectious diseases of birds and found that there have been few studies of the ecology of avian pathogens. Results suggest that global warming may increase the frequency with which avian diseases jump to humans, for example, by enabling tropical parasites such as malaria to spread north. The authors recommend that the control of diseases that are likely to appear as a result of climate change will require a network for testing wild birds for diseases.

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