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AN ANNOTATED CHECKLIST OF PATHOGENIC MICROORGANISMS ASSOCIATED WITH MIGRATORY BIRDS

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ABSTRACT: The potential for transport and dissemination of certain pathogenic microorganisms by migratory birds is of concern. Migratory birds might be involved in dispersal of microorganisms as their biological carriers, mechanical carriers, or as carriers of infected hematophagous ectoparasites (e.g., ixodid ticks). Many species of microorganisms pathogenic to homeothermic vertebrates including humans have been associated with free-living migratory birds. Migratory birds of diverse species can play significant roles in the ecology and circulation of some arboviruses (e.g., eastern and western equine encephalomyelitis and Sindbis alphaviruses, West Nile and St. Louis encephalitis flaviviruses), influenza A virus, Newcastle disease virus, duck plague herpesvirus, *Chlamydophila psittaci, Anaplasma phagocytophilum, Borrelia burgdorferi* sensu lato, *Campylobacter jejuni, Salmonella enterica, Pasteurella multocida, Mycobacterium avium, Candida* spp., and avian hematozoans. The efficiency of dispersal of pathogenic microorganisms depends on a wide variety of biotic and abiotic factors affecting the survival of the agent in, or disappearance from, a habitat or ecosystem in a new geographic area.

Key words: Arboviruses, bacteria, birds, fungi, migration, protozoa, viruses.

INTRODUCTION

A brief review of viruses and prokaryotic and eukaryotic microorganisms (bacteria, fungi, protozoa) pathogenic to homeothermic vertebrates and detected in migratory birds or in their ectoparasites is provided. It is well established that free-living birds, including migratory species, have the potential to disperse certain pathogenic microorganisms (Keymer, 1958; Pavlovsky and Tokarevich, 1966; McDiarmid, 1969; Davis et al., 1971; Lvov and Ilichev, 1979; Cooper, 1990; Hubálek, 1994; Nuttall, 1997; Wobeser, 1997). The potential for transport and dissemination of certain pathogenic microorganisms by migratory birds is of concern and is the subject of increased vigilance recently, stimulated by the occurrence and unprecedented spread of West Nile virus (WNV) in North America since 1999, where free-living birds have played a significant role (Anderson et al., 1999; Garmendia et al., 2000; Rappole et al., 2000; Bernard et al., 2001; Komar et al., 2002, 2003a; Dupuis et al., 2003; Male, 2003; Rappole and Hubálek, 2000).

Avian mobility and migration are remarkable biological phenomena, but they are also potentially crucial epizootiologic factors (Rosický, 1965; Nosek and Folk, 1977; Lvov and Ilichev, 1979). Even sedentary avian species can sometimes move as far as 50–100 km, and nomadic bird species can transport viable pathogens to distant sites during erratic movements. In addition, birds of diverse species often congregate at migration stops, where horizontal transmission of disease agents could occur from frequent interindividual and interspecies contacts.

Migratory birds are thought to be one of the mechanisms responsible for wide geographic distribution of certain important arboviruses (eastern equine encephalomyelitis [EEE] and Sindbis alphaviruses; WNV flavivirus), other viruses (influenza A and Newcastle disease viruses), bacteria (e.g., *Anaplasma phagocytophilum, Borrelia burgdorferi* s.l., *Campylobacter jejuni, Pasteurella multocida, Clostridium botulinum, Mycobacterium avium*), or protozoa (*Cryptosporidium baileyi*). The efficiency of this geographic dispersal depends, however, on a wide variety of biotic (e.g., susceptible local vertebrate recipients or invertebrate vectors, tenacity of the agent in the environment) and abiotic (temperature, humidity, etc.) factors affecting survival of the agent in a new environment.

Migratory birds could be involved in carriage of microbial pathogens by three mechanisms, including 1) as biological carriers, 2) as mechanical carriers, and 3) as hosts and carriers (transporters) of infected ectoparasites.

Biological carriers

Birds serve as biological carriers when the pathogen multiplies in the avian body. Infection of birds can be acute (e.g., in EEE, WNV, or Usutu virus infections; Newcastle disease; duck plague; ornithosis; mycoplasmal conjunctivitis; avian cholera; erysipelas), chronic (avian pox, avian tuberculosis, aspergillosis, leucocytozoonosis), latent, or asymptomatic (e.g., Sindbis or St. Louis encephalitis virus infection, influenza A, coxiellosis, Lyme borreliosis, campylobacteriosis, cholera, colibacillosis, salmonellosis, yersiniosis, listeriosis, candidosis, hemoproteosis, toxoplasmosis, sarcosporidiosis, cryptosporidiosis). The infected bird often sheds the agent, sometimes for a prolonged period (e.g., ornithosis, avian cholera). In some bird species (e.g., gulls) the shedding of a pathogen is more intense and clinical signs more obvious in younger birds than in adults (salmonellosis, cryptosporidiosis).

Mechanical carriers

Birds act as mechanical carriers when the pathogen does not multiply in or on the bird. This carriage can be either external, when the agent is located on the surface of the bird's body (e.g., fungal spores can survive for at least 12 days when inoculated on feathers of migratory swallows; Warner and French, 1970), or internal, when the agent passes through the digestive tract and is viable when excreted. For instance, it has been speculated that foot-and-mouth disease virus (FMDV) could be carried mechanically on free-living birds.

Carriers of infected hematophagous ectoparasites

Birds are hosts for many ectoparasites that sometimes serve as vectors of diseases. Of these, the most important are immature ixodid and argasid ticks that can be transported on their hosts from one site to another, even between continents (Ter-Vartanov et al., 1956; Černý and Balát, 1957; Hoogstraal et al., 1961, 1963, 1964; Nuorteva and Hoogstraal, 1963; Brinck et al., 1965; Kaiser et al., 1974; Nosek and Folk, 1977; Walter et al., 1979). Many tickborne pathogens can be carried this way: viruses (tickborne encephalitis viruses [TBE], Tyuleniy, Meaban, Bahig, Hughes group, Sakhalin group, Crimean-Congo hemorrhagic fever [CCHF] virus, Bhanja, Kemerovo, Great Island complex, Chenuda complex, Thogoto and Dhori viruses), bacteria (*Rickettsia* spp., *A. phagocytophilum, B. burdorferi* s.l.), and protozoa (*Babesia microti*). Surprisingly, fleas also can be transported over long distances on migrating birds (Ter-Vartanov et al., 1956; Schwan et al., 1983).

The mode of transport of pathogenic agents by migratory birds depends on the routes of transmission. In insectborne viruses, bacteria, and protozoa, duration and concentration of the agent in the blood of migrating birds is decisive for infection of competent insect vectors by feeding during stopover. In tickborne viruses, bacteria, and protozoa, the infectious larval or nymphal tick must remain attached for several days and then drop off during migration in a new geographic area. In waterborne infections, the agent can be shed by infected migrating birds, resulting in contamination of water with feces, nasal discharges, and respiratory exudates (e.g., influenza A virus, Newcastle disease virus [NDV], duck plague herpesvirus, *C. psittaci, Campylobacter, Salmonella, Escherichia, Vibrio cholerae, Yersinia* spp., *P. multocida, Enterococcus faecalis, Clostridium* spp.; *Candida* spp.). Also, pellets of migratory raptors or corvids are sometimes infected (e.g., *M. avium*). In addition, ingestion of infected carcasses of migratory birds can serve as the source of foodborne infection for local raptors, scavengers, and carnivorous mammals (e.g., WNV, *Clostridium* spp., *M. avium, Sarcocystis, Frenkelia*). Infections by inhalation can be caused by generation of contaminated aerosols by waterfowl flocks landing or taking flight (e.g., NDV or chlamydiosis). In contact infections, shedding of the agent from skin, feather pulp, or external lesions (e.g., avian pox, WNV encephalitis, mycoplasmal conjunctivitis) is another transmission strategy.

Seasonality is yet another important factor influencing effective transmission by migratory birds. For instance, mosquitoborne diseases in the Holarctic usually peak during late summer and early autumn (i.e., the season of maximum population density of many mosquito species). At the same time, waterfowl and wetland birds migrate and congregate on water reservoirs and in marshy areas, coming into close contact with ornithophilic vector mosquitoes (predominantly *Culex* spp.). In some mosquito species (usually *Aedes* spp.), a spring population peak occurs during the spring migration of birds. The coincidence of seasonality and location of migrating birds in flyways was observed in the 2002 WNV encephalitis epornitic in North America, where infection occurred in a spring outbreak in birds along the eastern and midwestern flyway, and then there was a second late summer outbreak as migrants moved south and across flyways. Even for some nonvectorborne pathogens, season plays a role. For instance, influenza A viruses remain infectious in water at lower ambient temperatures (i.e., from late autumn to early spring in the Holarctic) and at the same time major congregations of migratory waterfowl occur, increasing the probability of contact infection among birds.

Migration is a great stress on birds and resistance to infectious diseases might be diminished. In parallel, the shedding rate of an agent or duration and level of its viremia/bacteremia in already infected migrating birds might increase. There is some evidence for this effect. Migratory stress can induce *B. burgdorferi* s.l. spirochetemia and reactivate infection in redwing (*Turdus iliacus*; Gylfe et al., 2000), and WNV was isolated from several migrating young storks (*Ciconia ciconia*) that arrived in Israel in poor condition from eastern Europe (Malkinson et al., 2002). In addition, some avian hematozoans can be activated during the breeding season of their hosts, possibly by sex hormones (Haberkorn, 1968).

The number of pathogenic agents associated with migratory birds is probably greater than presently known, and continued research is therefore necessary. For instance, additional tickborne pathogens are probably being disseminated via carriage of infected larval and nymphal ixodid vectors on migratory birds. The widespread geographic distribution of *Francisella tularensis* or many rickettsiae might be explained by an occasional transport of infectious immature *Ixodes, Haemaphysalis,* or *Dermacentor* ticks parasitizing migratory birds, although the evidence (i.e., direct detection of the agents in the ticks attached to migrating birds) is still lacking.

CHECKLIST OF PATHOGENS CARRIED BY MIGRATORY BIRDS

Common English names of bird species, as well as geographic regions of their occurrence, can be found in Gruson (1976), whereas only scientific names are routinely used for avian species in this paper. Table 1 summarizes only important pathogens associated with migratory birds.

VIRUSES

Togaviridae: genus *Alphavirus*

Sindbis virus (syn. Ockelbo, Kyzyl-Agach; mosquitoborne): Isolated from migratory species *Motacilla alba* in India (Shah et al., 1960); *Streptopelia turtur* in Israel (Nir et al., 1967); *Ardeola ralloides* in Azerbaijan (Gaidamovich et al., 1968); *Gallinago gallinago* in Tajikistan (Gordee-

TABLE 1. Important microbial pathogens of homeothermic vertebrates associated with migratory birds.

Agent	Vector[a]	Association[b]	Distribution[c]	Avian disease
Togaviridae: *Alphavirus*				
Eastern equine encephalomyelitis (EEE)	Cul	PH	Am	EEE
Western equine encephalomyelitis (WEE)	Cul	PH	Am	WEE
Sindbis	Cul	PH	Afr, Eur, As, Aus	
Flaviviridae: *Flavivirus*				
St. Louis encephalitis	Cul	PH	Am	
West Nile virus (WNV)	Cul	PH	Afr, Eur, As, Am	WNV encephalitis
Japanese encephalitis	Cul	PH	As	
Tickborne encephalitis (TBE) group	Ixo	T, OH	Eur, As	Louping ill, TBE
Bunyaviridae: *Nairovirus*				
Crimean-Congo hemorrhagic fever	Ixo	T	Eur, As, Afr	
Reoviridae: *Orbivirus*				
Kemerovo	Ixo	OH	As, Afr	
Orthomyxovirdae				
Influenzavirus A		PH	Worldwide	Avian influenza
Paramyxoviridae: Paramyxovirus				
Newcastle disease virus		PH	Worldwide	Newcastle disease
Adenoviridae				
Aviadenovirus galli-1		PH	Worldwide	Egg-drop syndrome
Poxviridae				
Avipoxvirus		PH	Worldwide	Avian pox
Herpesviridae				
Herpesvirus anatis		PH	Am, Eur	Duck plague
Rickettsiales				
Rickettsia sibirica	Ixo	OH, T	As	
Coxiella burnetii	(Ixo)	OH (T)	Worldwide	
Anaplasma phagocytophilum	Ixo	T, OH	Holarctic	
Chlamydiaceae				
Chlamydophila psittaci		PH	Worldwide	Ornithosis
Mycoplasmataceae				
Mycoplasma gallisepticum		OH	Am	Mycoplasmosis
Spirochaetaceae				
Borrelia burgdorferi s.l.	Ixo	OH, T	Holarctic	
Campylobacteraceae				
Campylobacter jejuni		PH	Worldwide	Campylobacteriosis
Vibrionaceae				
Vibrio cholerae		OH	Am	
Enterobacteriaceae				
Escherichia coli (enteropathogenic)		OH	Worldwide	Colibacillosis
Salmonella enterica		OH	Worldwide	Salmonellosis
Yersinia enterocolitica		OH	Eur, As	
Y. pseudotuberculosis		OH	Worldwide	Pseudotuberculosis
Pasteurellaceae				
Pasteurella multocida		PH	Worldwide	Avian cholera
Riemerella anatipestifer		PH	Worldwide	New duck disease

TABLE 1. Continued.

Agent	Vector[a]	Association[b]	Distribution[c]	Avian disease
Gram-positive cocci				
Staphylococcus aureus		OH	Worldwide	Staphylococcosis
Enterococcus faecalis		OH	Eur	
Endospore-forming gram-positive rods				
Clostridium botulinum		OH	Worldwide	Avian botulism
C. perfringens		OH	Worldwide	Necrotic enteritis
Regular nonsporing gram-positive rods				
Listeria monocytogenes		OH	Eur, As	Listeriosis
Erysipelothrix rhusiopathiae		OH	Am, As	Erysipelas
Mycobacteriaceae				
Mycobacterium avium		PH	Worldwide	Avian tuberculosis
Endomycetes				
Candida albicans		OH	Worldwide	Candidosis
C. tropicalis		OH	Worldwide	
Hyphomycetes				
Aspergillus fumigatus		OH	Worldwide	Aspergillosis
Piroplasmida				
Babesia microti	Ixo	T	Holarctic	
Haemosporina				
Plasmodium spp.	Cul	PH	Worldwide	Avian malaria
Leucocytozoon simondi	Sim	PH	Holarctic	Leucocytozoonosis
Haemoproteus spp.	Dip	PH	Worldwide	Hemoproteosis
Eimeriina				
Toxoplasma gondii		OH	Worldwide	Toxoplasmosis
Eimeria spp.		PH	Worldwide	Coccidiosis
Sarcocystis spp.		PH	Worldwide	Sarcosporidiosis
Cryptosporidium spp.		OH	Worldwide	Cryptosporidiosis
Kinetoplastida				
Trypanosoma avium	Dip	PH	Worldwide	

[a] Principal vector of the agent: Cul = mosquitoes; Ixo = ixodid ticks; Sim = simuliids; Dip = other biting diptera.
[b] Association with migratory birds: PH = principal biological hosts; OH = occasional (or mechanical) hosts; T = transport of infected ectoparasites.
[c] Am = Americas; Afr = Africa; Eur = Europe; Aus = Australia; As = Asia.

va, 1980); *Acrocephalus scirpaceus, Vanellus vanellus,* and *Sturnus vulgaris* in Slovakia (during spring migration; Ernek et al., 1973, 1977); and migrating birds in Estonia (Uryvaev et al., 1992). It is most probable that the causative agent of Ockelbo disease ("Pogosta," "Karelian fever"; i.e., Sindbis virus) was introduced to Fennoscandia from subtropical regions by migratory birds (Hubálek, 1994).

Eastern and western equine encephalitis viruses (mosquitoborne): Repeatedly isolated from North American birds actively migrating (Stamm and Newman, 1963; Lord and Calisher, 1970; Calisher et al., 1971). Eastern equine encephalitis virus was also isolated from southward-migrating birds (*Colaptes auratus, Icterus galbula, Zonotrichia albicollis*) in eastern Long Island (New York, USA); the migrants were thought responsible for initiating a small local EEE epizootic (Bast et al., 1973; Morris et al., 1973). Eastern equine encephalitis virus was also isolated from several trans-Gulf migrants (*Icterus spurius, Dendroica striata, Hylocichla* *mustelina*). The 1962 epidemic of EEE in Jamaica probably resulted from the transport of EEE virus by birds from continental USA (Work and Lord, 1972).

Venezuelan equine encephalitis virus (VEE): Suspected of being transported from South to Central America. Experimental data on migratory birds confirmed that they are effective amplifying hosts with moderate to high levels of viremia for 2–4 days postinoculation, sufficient to infect vector mosquitoes (Dickerman et al., 1980). Tonate virus is antigenically related to VEE virus; it was isolated from birds and mosquitoes in French Guiana, and then from cimicid bugs (*Oeciacus vicarius*) parasitizing *Petrochelidon pyrrhonota* and *Passer domesticus* in the USA (Monath et al., 1980). The isolation of this virus in the USA might reflect its introduction by migratory birds from South America.

Mayaro virus (mosquitoborne): Occurs in South and Central America, but it was also isolated from a migrating bird in the USA north of the area of virus distribution (Calisher et al., 1974).

Semliki Forest virus (mosquitoborne): Isolated from a northward-migrating *Motacilla flava* in Kazakhstan (Lvov and Ilichev, 1979).

Flaviviridae*: genus *Flavivirus

Japanese encephalitis virus (JEV; mosquitoborne): Amplifies well in colonial ardeids *Nycticorax* and *Egretta* spp. (Buescher et al., 1959; Scherer et al., 1959; Boyle et al., 1983); movements of these birds, including migration, provide a means for dispersal of the mosquitoborne JEV far beyond the area of avian colonies.

West Nile virus: Colonial and other birds are significant in the circulation of this virus. Nestlings could represent ideal blood donors for ornithophilic *Culex* mosquitoes and might serve as amplifying hosts of the virus. West Nile virus was isolated from migrating *Sylvia nisoria* in Cyprus (Watson et al., 1972); *S. turtur, M. alba,* and *C. ciconia* in Israel (Nir et al., 1967; Malkinson et al., 2002); *Tringa ochropus, V. vanellus, Larus ridibundus,* and *S. turtur* just arriving to Slovakia from their winter ranges (Ernek et al., 1977); and *Sterna albifrons* in Tajikistan (Gordeeva, 1980), as well as from other migratory species in Europe or elsewhere, including *A. ralloides, Ixobrychus minutus, Botaurus stellaris, Plegadis falcinellus, Anas platyrhynchos, A. querquedula, Fulica atra, Larus cachinnans, Corvus frugilegus, Corvus corone, Pica pica, S. vulgaris,* and *Turdus merula* (Hubálek, 1994). A large number of avian species, many of them migratory (including, e.g., *Corvus brachyrhynchos, Cyanocitta cristata, Larus* spp.), are hosts of WNV in North America (Bernard et al., 2001), and the virus was isolated at high titers from oral and cloacal swabs of dead *C. brachyrhynchos,* and *C. cristata* (Komar et al., 2002). A surprisingly high mortality occurs in some WNV-infected North American birds compared with Old World avian species, and some bird populations could be endangered because of this infection (Anderson et al., 1999; Garmendia et al., 2000; Male, 2003). Experimental studies have shown that many North American species are competent (i.e., virus amplifying) hosts for WNV (e.g., *C. brachyrhynchos, C. ossifragus, C. cristata, Quiscalus quiscula, Carpodacus mexicanus, Larus delawarensis*), attaining high viremias between 1 and 7 days postinoculation (Komar et al., 2003a). A plausible hypothesis supposes dispersal (and reintroductions) of WNV by migratory birds between Africa, southern Asia, and Europe (Hannoun et al., 1972; Lvov and Ilichev, 1979; Hubálek, 1994; Malkinson et al., 2002), as well as recent, rapid long-distance dispersal of WNV over the North American continent, Mexico, and the Caribbean (Rappole et al., 2000; Dupuis et al., 2003; Komar et al., 2003b). Additional movements of competent nonmigratory birds like *P. domesticus* (Rappole and Hubálek, 2000) or short-distance migrants (*C. brachyrhynchos, C. cristata, Q. quiscula*) could be responsible for lateral geographic spread of WNV outside the main migratory routes of birds in North America. For instance, *C. brachyrhynchos* use regular communal roosts, and their daily flights from the nocturnal roost to feeding sites might range up to 20–30 km; the crows feeding on infectious carcasses of birds might spread WNV through a chain of neighboring corvid roosts.

Usutu virus: Related to WNV and previously isolated only in South Africa, caused an epornitic among *T. merula* in Austria during late summers in 2001–03 (Weissenböck et al., 2002).

St. Louis encephalitis virus (SLEV): American mosquitoborne *Flavivirus,* also related to WNV, was isolated many times from free-living (including migratory) birds, which are its principal amplifying hosts. These birds have moderate levels of viremia sufficient to infect vector mosquitoes. Several SLEV isolations were obtained from migratory bird species in the Caribbean and Amazon basin (Theiler and Downs, 1973).

Tickborne encephalitis (TBE) complex viruses: Birds can disseminate TBE viruses (Central European encephalitis, Russian spring-summer encephalitis, louping ill) by transporting infected ixodid ticks. For instance, two strains of TBE virus were recovered from nymphal *Ixodes ricinus* collected on *T. merula* in Slovakia (Ernek et al., 1968).

Omsk hemorrhagic fever (OHF) and Kyasanur Forest disease (KFD): Antigenically closely related and are also related to TBE viruses. It has been hypothesized that the tickborne KFD virus might be a variant of OHF virus after transport to the Indian subcontinent by migratory birds (Work, 1958). Some avian sera in Siberia have been positive for KFD virus antibodies (Matukhin and Fedorova, 1969).

Tyuleniy virus: Occurs in *Ixodes uriae* ticks inhabiting nests of seabirds and it is transported by the birds (Lvov and Ilichev, 1979).

Meaban virus: Isolated from *Ornithodoros maritimus* ticks collected in nests of *Larus argentatus* in France; the virus is closely related to Australasian Saumarez Reef virus and could have been introduced to France by *Sterna paradisaea* terns (Chastel, 1988).

Bunyaviridae*: genera *Bunyavirus, Nairovirus

Simbu group bunyaviruses (mosquitoborne): Ingwavuma virus was isolated from two northward-migrating *Muscicapa striata* in Cyprus, and Thimiri virus from *Sylvia curruca* and *S. communis* migrating southwards in Egypt (Watson et al., 1972).

Tete group bunyaviruses: A total of 41 isolations of Bahig virus and 57 isolations of Matruh virus were made from south-migrating Eurasian birds in Egypt and Cyprus (Watson et al., 1972; Hoogstraal, 1976); prevailing hosts were *Sylviidae, Fringillidae,* and *Turdidae.* Bahig virus was also recovered from larval *Hyalomma marginatum rufipes* ticks (an African subspecies) parasitizing a northward-migrating *Oenanthe oenanthe* in Egypt (Converse et al., 1974).

Hughes group nairoviruses: Hughes, Punta Salinas, Soldado, and Zirqa occur in argasid ticks (*Ornithodoros capensis* group) living in seabird nests (Varma et al., 1973; Yunker, 1975; Nuttall et al., 1984, 1986; Chastel, 1988). Marine bird migrations undoubtedly account for the remarkably extensive geographic distribution of Soldado virus and other arboviruses of this serogroup.

Sakhalin group nairoviruses: Avalon (syn. Paramushir) and Clo Mor viruses were isolated from *I. uriae* ticks in colonies of marine birds, and all the Sakhalin group viruses can be transported by seabirds in the subpolar regions (Lvov et al., 1975; Yunker, 1975; Main et al., 1976).

Crimean-Congo hemorrhagic fever nairovirus: Birds could disseminate the virus long distances by the transport of infected immature *H. marginatum, Haemaphysalis punctata,* or other amblyommine ticks (Hoogstraal, 1979); antigenic and genomic identity of the CCHF strains from Africa and Eurasia is striking.

Bhanja virus: As for CCHF virus, migratory birds are regarded as carriers of infected immature amblyommine ticks (Hubálek et al., 1982).

Reoviridae: genus *Orbivirus*

Kemerovo virus (tickborne): Isolated from a southward-migrating *Phoenicurus phoenicurus* in Egypt (Schmidt and Shope, 1971), this strain (EgAr 1169-61) was indistinguishable from Siberian isolates by antigenic and RNA molecular studies, suggesting the redstart might have acquired the virus in Siberia and that migratory birds are involved in its dispersal over very long distances.

Other orbiviruses of the Great Island antigenic complex (Bauline, Great Island, Cape Wrath, Mykines, Tindholmur) have been isolated from *I. uriae* ticks inhabiting seabird nests (Main et al., 1973; Doherty et al., 1975; Yunker, 1975; Calisher et al., 1988). These viruses occur in both subantarctic and subarctic regions and are obviously dispersed transoceanically and introduced by seabirds to new areas and new avian hosts.

Chenuda complex orbiviruses: Baku, Chenuda, Mono Lake, etc. have been isolated repeatedly from ticks associated with migratory gulls (Lvov and Ilichev, 1979; Schwan et al., 1988).

Orthomyxoviridae: genera *Thogotovirus, Influenzavirus*

Thogoto and Dhori viruses: Suspected of being introduced occasionally by preimaginal amblyommine ticks on migratory birds from Africa and/or South Asia to southern Eurasia (Filipe and Casals, 1979; Calisher et al., 1987).

Influenza A virus: Often isolated from migratory birds, including ducks, geese, gulls, terns, shearwaters, guillemots, and, less often, shorebirds and passerine species from throughout the world (Stallknecht and Shane, 1988; Alexander, 2000; Fouchier et al., 2003). Wild aquatic birds are regarded as the principal reservoir of influenza viruses, and migrating ducks disseminate influenza viruses worldwide (Hinshaw and Webster, 1982; Webster et al., 1992). These viruses can adapt to new host species (Suarez, 2000). All of the antigenic subtypes of influenza A viruses (H1–H14 and N1–N9) are perpetuated in aquatic birds, particularly in migrating waterfowl (Hinshaw et al., 1980). Isolation rate of influenza virus from migratory ducks ranges from 0.3% to 30% (Bahl et al., 1977; Slemons and Easterday, 1977; Hinshaw et al., 1985; Slemons et al., 1991). In Europe, approximately 1–5% of migratory geese, mallards, and other dabbling ducks carry and shed the virus even in the winter (De Marco et al., 2003).

Paramyxoviridae: genus *Rubulavirus*

Newcastle disease virus (NDV, avian parainfluenza virus 1, paramyxovirus-1): Isolated from many species of free-living birds (Wobeser, 1997), including a migrating *Upupa epops* in India (Sharma and Baxi, 1980). Infected birds can transport the virus over long distances because recovered avian hosts and immune carriers can shed the virus indefinitely (Davis et al., 1971).

Picornaviridae: genus *Aphthovirus*

Foot-and-mouth disease virus: Several authors have suggested that FMDV can be dispersed with birds as mechanical carriers and even introduced with migrants (*S. vulgaris, C. frugilegus, Larus* spp.) from continental Europe to the British Isles (Eccles, 1939; Hurst, 1968; McDiarmid, 1969; Kaleta, 2002). However, direct evidence for long-distance mechanical transport of FMDV by birds is lacking.

Adenoviridae: genus *Aviadenovirus*

Egg drop syndrome virus: Causes high fragility of egg shells and a lower fertility in fowl and anseriforms. Antibodies against this virus were detected in migratory ducks, coots, and grebes in Europe, Israel, and USA (Kaleta et al., 1980; Malkinson and Weisman, 1980; Gulka et al., 1984). The virus can be disseminated by migratory anseriform species.

Herpesviridae

Anatid herpesvirus 1: Causes duck virus enteritis (duck plague) in many species of wild anseriforms (ducks, geese, swans) in North America and Europe with a high mortality. The virus was carried by healthy migratory waterfowl (*Branta canadensis, Anas* spp.) as long as 4 yr after infection (Wobeser, 1997).

Poxviridae: genus *Avipoxvirus*

At least 10 species of *Avipoxvirus* have been described in about 232 avian species (Bolte et al., 1999). Many of them affect migratory avian species and can thus be dispersed into distant localities.

BACTERIA

Rickettsiaceae, Anaplasmataceae

Rickettsia sibirica: The agent of North-Asian tick typhus, it was isolated from *Haemaphysalis concinna* ticks collected on birds in the Far East (Somov and Soldatov, 1964). The role of wild birds in the epizootiology of this tickborne rickettsiosis is much lower than that of mammals but the establishment of new foci of the disease through birds carrying infected ixodid ticks has been suggested.

Coxiella burnetii: The agent of Q-fever, it was isolated from many species of wild birds, including migratory *Hirundo rustica, P. phoenicurus,* and *M. alba* in Czechland (Syrůček and Raška, 1956). The birds can maintain viable coxiellae in their kidneys for several weeks while seronegative.

Anaplasma phagocytophilum: The agent of human granulocytic ehrlichiosis (anaplasmosis), it can be carried in immature *Ixodes scapularis* or *I. ricinus* vector ticks attached to migrating birds, as was detected in North America (Daniels et al., 2002), Sweden (Bjoersdorf et al., 2001), and Russia (Alekseev et al., 2001).

Chlamydiaceae

Chlamydophila psittaci: Causes ornithosis (chlamydiosis, psittacosis) in birds of 30 orders, including migratory species of waterfowl, gulls, terns, shorebirds, pigeons, passerines, etc. (Kaleta and Taday, 2003). Wild ducks, gulls, egrets, grackles, and other bird species present a significant reservoir of ornithosis and can spread the disease by direct contact or via infectious aerosol to vertebrates and can introduce it to new localities (Davis et al., 1971; Page, 1976; Grimes et al., 1979; Lvov and Ilichev, 1979; Brand, 1989). Some chlamydial strains not normally pathogenic to wild avian hosts can be highly virulent for domestic fowl and humans.

Mycoplasmataceae

Mycoplasma gallisepticum: The agent of mycoplasmal conjunctivitis in passerines (*Carpodacus mexicanus, Carduelis tristis*), it is recently spreading through the USA westward (Hartup et al., 2001). However, this is probably a wave of disease transmission passed from one site to another by nonmigratory rather than migratory avian species, possibly similar to the lateral or westward spread of WNV over North America. Nonetheless, *M. gallisepticum* was also isolated from a short-distance migrant, *Uria aalge,* in Germany (Petermann et al., 1989). *Mycoplasma synoviae* was isolated from a dead juvenile *Rissa tridactyla* in Brittany, France (Kempf et al., 2000), and *Mycoplasma cloacale* from migratory *Aythya fuligula, Alauda arvensis,* and *S. vulgaris* in Great Britain and France (Bradbury et al., 1987).

Spirochaetaceae

Borrelia burgdorferi sensu lato genomic species (B. burgdorferi sensu stricto, B. garinii, B. valaisiana, but not B. afzelii): The causative agents of tickborne Lyme disease, which have been detected often in *Ixodes* ticks parasitizing birds, including migratory species (Anderson and Magnarelli, 1984; Magnarelli et al., 1992; Humair et al., 1993; Hubálek, 1994; Olsén et al., 1995b; Hubálek et al., 1996; Daniels et al., 2002; Hanincová et al., 2003; etc.). In the *I. ricinus* complex, transovarial infection rate with *B. burgdorferi* s.l. is <5%; several surveys, however, found the infection rate of larval ixodid ticks feeding on certain bird species (e.g., thrushes, family *Turdidae*) to be >10% (Humair et al., 1993; Hubálek et al., 1996; Hanincová et al., 2003); this means that some larval ticks were infected either from the spirochetemic host or via a so-called cofeeding mechanism (Gern and Rais, 1996). In one study, 22% of 250 preimaginal *I. scapularis* collected from 58 mainly ground-foraging birds in Wisconsin (USA) were positive for *B. burgdorferi,* and nearly half of the spirochete-positive ticks were removed from migrating birds (Weisbrod and Johnson, 1989). Some avian migratory species are reservoirs of borreliae (*B. burgdorferi* s.l.; Anderson and Magnarelli, 1984; Olsén et al., 1993). *Borrelia garinii* repeatedly has been isolated from *I. uriae* collected in nests of colonial seabirds in the Baltic and North seas and from the birds (*Alca torda, Fratercula arctica*) themselves (Olsén et al., 1993, 1995a; Gylfe et al., 1999). An experimental study (Burgess, 1989) showed that *A. platyrhynchos* infected with *B. burgdorferi* s.s. remained asymptomatic, but the spirochete was recoverable from the blood for 7 days postinoculation and from the cloaca content for 3–4 wk postinoculation. Migratory birds are therefore a natural means for distribution of the spirochete over long distances (Olsén et al., 1995). For instance, the North American geographic range of Lyme disease seems to parallel known bird migration flyways.

Campylobacteraceae

Campylobacter jejuni: Main agent of intestinal campylobacteriosis, it is the most frequently isolated campylobacter species from a wide variety of aquatic and terrestrial wild birds. Thirty-five percent of migrating ducks tested harbored this organism (Luechtefeld et al., 1980), as well as 4–63% of *Larus* spp., 6% of *Sterna hirundo* in Norway (Kapperud and Rosef, 1983), and many *L. ridibundus* in Sweden (Broman et al., 2002). *Campylobacter* spp. were isolated from other migratory species, including *V. vanellus, Milvus milvus, F. atra, Gallinula chloropus,* and *C. frugilegus* in Germany (Glünder, 1989). Less frequently, *Campylobacter* species (*C. coli* and *C. laridis*) are isolated from birds (Glünder and Petermann, 1989; Quessy and Messier, 1992; Sixl et al., 1997). The carrier state of young *L. argentatus* for *C. jejuni* lasted about 3–4 wk (Glünder et al., 1992). Migratory seagulls have been implicated in the spread of campylobacters to domestic animals or humans via feedstuffs or water (Sacks et al., 1986).

Vibrionaceae

Vibrio cholerae: Isolated occasionally from free-living waterbirds (Lee et al., 1982) e.g. from 17% of fecal samples collected from 1,131 aquatic birds in Colorado and Utah (USA; Ogg et al., 1989). The latter study suggests that migratory waterfowl serve as disseminators of *V. cholerae* (three serotype O1 biovar 'eltor' subtype Ogawa isolates were recovered from *Ardea herodias* and *L. delawarensis*); they might have transported the organism to Colorado from a focus where O1 serotype persists, such as estuaries along the Gulf Coast and Chesapeake Bay. Avian droppings contaminating a water supply or inland surface waters with the epidemic strain of *V. cholerae* could thus cause cholera outbreaks far from areas where cholera is endemic. Non-O1 *V. cholerae* have also been isolated from gulls (Lee et al., 1982; West et al., 1983; Buck, 1990).

Enterobacteriaceae

Escherichia coli: Enteropathogenic strains, such as the vero cytotoxin-producing O157:H7 strain, are the agent of colibacillosis and have been isolated from healthy or diseased wild birds, including migrants such as *Ardea cinerea, B. canadensis, Cygnus columbianus, U. aalge,* and *Columba palumbus* (Hubálek, 1994; Wallace et al., 1997). They can become carriers of *E. coli* strains resistant to antibiotics and can be responsible for the spread of R plasmids over a wide area (Kanai et al., 1981).

Salmonella enterica: Numerous serovars (particularly Typhimurium, Enteritidis, Derby, Panama) of *S. enterica* have been isolated often from many species of free-living birds, including migrants (largely gulls, but also ducks, terns, and some passerines). There is a voluminous literature on this subject (Davis et al., 1971; Fenlon, 1981; Coulson et al., 1983; Hubálek, 1994; Refsum et al., 2002; Hernandez et al., 2003). Moreover, multidrug-resistant strains of *S. enterica* Typhimurium were detected in migrating birds in Sweden (Palmgren et al., 1997).

Yersinia enterocolitica: Isolated from fecal samples of gulls and terns in Norway (Kapperud and Rosef, 1983), ducks and *Sturnus cineraceus* in Japan (Kawaoka et al., 1984; Kato et al., 1985; Kaneuchi et al., 1989), and many migratory species in the USA (Shayegani et al., 1986) and Sweden (Niskanen et al., 2003).

Yersinia pseudotuberculosis: Can cause mortality in wild birds, especially during severe winter conditions; the bacterium was isolated from migrating *M. alba, Emberiza spodocephala, Anas poecilorhyncha, A. penelope, L. ridibundus,* and *L. crassirostris,* as well as from seabirds and shorebirds in Japan (Hamasaki et al., 1989; Kaneuchi et al., 1989; Fukushima and Gomyoda, 1991); *S. vulgaris* in France; and many migratory species in Sweden (Niskanen et al., 2003). In Japan, the most common *Y. pseudotuberculosis* serovars from wild ducks were 1b and 4b, which were also the most frequent serovars isolated from humans (Hamasaki et al., 1989; Fukushima and Gomyoda, 1991).

Pasteurellaceae

Pasteurella multocida: The agent of avian cholera, an important, highly contagious disease that can cause significant mortality in wild waterfowl (Davis et al., 1971; Hubálek, 1994; Wobeser, 1997). For example, as many as 72,000 migratory ducks and geese died in the Central and Mississippi flyways in North America during the 1979–80 outbreak that originated in the breeding range of migratory *Anser caerulescens* along the western Hudson Bay in summer 1979 (Brand, 1984). Avian cholera outbreaks are promoted by dense local bird concentrations, and *P. multocida* can survive in water (especially alkaline water) for several days to weeks. Some ducks that recover from the infection might serve as long-term carriers of the agent (Hunter and Wobeser, 1980); thus, the bacterium might be transferred by the birds to distant wetland locations. Pasteurellosis was also found in many other migratory species of birds in Europe and North America (*Phoenicopterus ruber, L. ridibundus, L. argentatus, V. vanellus, Apus apus, H. rustica, Turdus pilaris, T. merula, T. philomelos, T. migratorius, Erithacus rubecula, Bombycilla* spp., *C. corone, P. pica,* and *S. vulgaris*; Macdonald et al., 1981; Hubálek, 1994; Wobeser, 1997).

Riemerella anatipestifer (formerly Pasteurella): The agent of septicemia of young waterfowl, it was isolated from normal *B. canadensis* in Canada (Wobeser, 1997) and from migratory *L. ridibundus* (Hinz et al., 1998) and *R. tridactyla* (Petermann et al., 1989) in Germany.

Francisella tularensis: Migratory birds might play a role in dispersal of tularemia via infected, attached ixodid ticks (Hubálek, 1994).

Gram-positive cocci

Staphylococcus aureus: Isolated from excreta of seagulls (Cragg and Clayton, 1971; Wood and Trust, 1972), corvids (Golebiowski, 1975; Hájek et al., 1991), and other migratory birds (Keymer, 1958; Sambyal and Baxi, 1980).

Enterococcus faecalis: Vancomycin-resistant enterococci were isolated from a fecal sample of a north-migrating *L. ridibundus* in southern Sweden in March 1998; few other strains were isolated from gulls at sub-Antarctic Bird Island in 1996 (Sellin et al., 2000).

Endospore-forming Gram-positive rods

Clostridium botulinum: Birds disperse *C. botulinum* spores to adjacent or distant water reservoirs (Hill and Graham, 1961; Matveev and Konstantinova, 1974; Hussong et al., 1979), where they can germinate and cause avian botulism, a major disease of wild waterfowl (Hubálek, 1994; Wobeser, 1997).

Clostridium perfringens: Isolated from dead pelicans and marine birds in Florida (USA; Ankerberg, 1984), other wild birds (waterfowl, shorebirds, raptors, *T. migratorius*) with necrotizing enteritis in the USA, *A. cinerea,* dead gulls, and *U. aalge* in Germany (Petermann et al., 1989; Hubálek, 1994; Wobeser, 1997).

Regular nonsporing Gram-positive rods

Listeria monocytogenes: Gulls feeding at Scottish sewage works had a high rate (15%) of carriage of the agent (Fenlon, 1985) and the bacterium has been isolated from *C. frugilegus* in France (Bouttefroy et al., 1997). Other migratory birds (*Falco columbarius, S. vulgaris, E. rubecula, Anthus trivialis*) also yielded the agent and might thus play a role in dispersal of listeriae (Macdonald, 1968; Hubálek, 1994).

Erysipelothrix rhusiopathiae: The agent of erysipelas, it can cause epornitics (*Podiceps nigricollis,* Jensen and Cotter, 1976) or sporadic cases in wild, mainly waterbirds, including migratory species such as mergansers, ducks, geese, storks, gulls, cranes, etc. (e.g., Davis et al., 1971; Wobeser, 1997).

Mycobacteriaceae

Mycobacterium avium: Pathogenic to many wild avian species (tuberculosis is one of the most widespread wild avian infections) can be carried by some migratory birds, such as raptors, *C. palumbus,* or *C. frugilegus* (Davis et al., 1971; Smit et al., 1987; Hejlíček and Treml, 1993; Hubálek, 1994; Wobeser, 1997).

FUNGI

Yeasts and yeast-like fungi

Candida albicans: Has been often isolated from the digestive tract or excreta of migratory gulls (van Uden and Castelo-Branco, 1963; Kawakita and van Uden, 1965; Cragg and Clayton, 1971; Buck, 1983, 1990). A gull experimentally fed fish containing *C. albicans* shed the yeast heavily in feces over 13 days postinoculation, and for 40 days postinoculation, it excreted the yeast sporadically, despite being treated with ketoconazole (Buck, 1986). The gulls might thus serve as carriers, disseminators, or even reservoirs of *C. albicans.*

Candida tropicalis: Isolated repeatedly from excreta of migratory gulls and terns along the coast of Portugal (van Uden and Castelo-Branco, 1963; Kawakita and van Uden, 1965).

Hyphomycetes

Aspergillus fumigatus: The causative agent of avian and mammalian aspergillosis, it was isolated from throat swabs of migratory waterbirds: 7% of *Anser brachyrhynchus,* 7% of *B. canadensis,* and 13% of *L. argentatus* (Beer, 1963). *Aspergillus fumigatus* was detected on the feathers of 11% and 17% of wild birds examined in Britain and Czechland, respectively (Hubálek, 1994). However, this fungus is a cosmopolitan, ubiquitous species, and the role of migratory birds in its dispersal is uncertain.

A number of other pathogenic fungi have been detected on feathers of migratory birds, including *Aspergillus flavus, A. nidulans, Microsporum gypseum, M. ripariae, M. persicolor,* and *Trichophyton mentagrophytes* (Hubálek, 1994).

PROTOZOA

Piroplasmida

Babesia microti: The agent of human babesiosis, it might be dispersed by migratory birds via attached, infected nymphal and larval *Ixodes* ticks (Alekseev and Dubinina, 2003).

Haemosporina

Leucocytozoon simondi: A parasite of many Holarctic anseriform species transmissible by blackflies (*Simuliidae*), it is pathogenic to ducklings and goslings. Interestingly, the protozoan was originally described in *Anas crecca* wintering in Vietnam (Mathis and Leger, 1910), but probably breeding in northern Asia.

Haemoproteus: Currently, total of 128 species of *Haemoproteus* include avian hematozoans that are relatively benign and not known to cause serious harm to birds in that they coevolved with their avian hosts (Bennett, 1993). Many species of *Haemoproteus* are transmitted by hematophagous ceratopogonid or hippoboscid biting flies. *Haemoproteus* spp. are quite common in migratory species (e.g., *Phylloscopus trochilus* in Scandinavia [Bensch and Akesson, 2003] or anatids in North America [Bennett et al., 1974, 1975]). During the autumn migration of *Fringilla coelebs* along the Baltic Sea, the last wave of the migrating birds was observed to be most heavily infected with *Haemoproteus fringillae* and probably delayed in migration because of acute illness (Valkiunas, 1989, 1991).

Plasmodium relictum, P. circumflexum, and P. vaughani: Cause mosquitoborne avian malaria, which can result in mortality. These protozoa also have been found in some migratory species, including passerines, pigeons, anatids, and raptors (McDiarmid, 1969; Bennett et al., 1974, 1975). *Plasmodium* is quite common in migratory *P. trochilus* in Scandinavia (Bensch and Akesson, 2003). Chronically infected migratory birds returning from their winter ranges could initiate summer transmission of these parasites.

Eimeriina

Toxoplasma gondii: Was recorded in, or isolated from, many migratory species, including ducks, raptors, *L. ridibundus, S. vulgaris, C. frugilegus,* and *C. monedula* (Pak, 1976; Haslett and Schneider, 1978; Lvov and Ilichev, 1979; Literák et al., 1992). Infected birds might be less mobile and more susceptible to predation by felids (Hubálek, 1994).

Eimeria, Isospora: Coccidia occur in many birds, including migratory species like raptors or seabirds (Petermann et al., 1989). For instance, *E. boschadis, E. somateriae,* and *E. truncata* are renal coccidia of wild ducks and geese, and infection can occasional result in fatalities. These parasites are distributed by migratory waterfowl (Nation and Wobeser, 1977; Gajadhar et al., 1983; Wobeser, 1997). Other coccidia, *E. aythyae, E. bucephalae,* and *E. anseris* cause severe intestinal coccidiosis of diving ducks and geese (Gajadhar et al., 1983; Wobeser, 1997).

Sarcocystis, Frenkelia: Sarcosporidiosis has been detected in adult avian intermediate hosts (definitive hosts are carnivores). Migratory ducks (2–65% adult ducks) are parasitized by *S. rileyi* in North America (Wobeser, 1997). Other migratory birds affected are herons, columbids, gulls, corvids, and swallows (McDiarmid, 1969; Spalding et al., 1994; Wobeser, 1997). Definitive hosts for *Frenkelia microti* include migratory *Buteo buteo* in Europe and *Buteo jamaicensis* in North America (Upton and McKown, 1992; Hubálek, 1994).

Cryptosporidium baileyi: An enteric intracellular coccidian parasite that can cause gastrointestinal and respiratory tract disorders or, more often, subclinical and asymptomatic infections in birds. *Cryptosporidium* oocysts were found in feces and cloacal samples of migratory gulls in Scotland (*L. argentatus, L. ridibundus*; Smith et al., 1993) and Czechland (*L. ridibundus*; Pavlásek, 1993). Infectious cryptosporidial oocysts were found in feces of migratory *B. canadensis* in Maryland (USA; Graczyk et al., 1998). Waterbirds can thus disseminate cryptosporidia in the environment.

Kinetoplastida

Trypanosoma everetti: Observed in Britain in migratory passerine species that were obviously infected on their African winter range (Peirce and Mead, 1984). *Trypanosoma avium* and related avian trypanosomes are largely nonpathogenic to their hosts but can occasionally cause mild disease in young birds; they are usually transmitted by hippoboscid flies, blackflies, or biting midges (Hubálek, 1994).

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