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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 epizootologic

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 af-

fecting 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 tick-borne pathogens can be carried this way: viruses (tickborne encephalitis viruses [TBE], Tyulenyi, Meaban, Bahig, Hughes group, Sakhalin group, Crimean-Congo hemorrhagic fever [CCHF] virus, Bhanja, Kemerovo, Great Island complex, Chenu-da 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, in-

gestion 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, mosquito-borne 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 epidemic 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 vi-

remia/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 (Haberkm, 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
<i>Togaviridae: Alphavirus</i>				
Eastern equine encephalomyelitis (EEE)	Cul	PH	Am	EEE
Western equine encephalomyelitis (WEE)	Cul	PH	Am	WEE
Sindbis	Cul	PH	Afr, Eur, As, Aus	
<i>Flaviviridae: Flavivirus</i>				
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
<i>Bunyaviridae: Nairovirus</i>				
Crimean-Congo hemorrhagic fever	Ixo	T	Eur, As, Afr	
<i>Reoviridae: Orbivirus</i>				
Kemerovo	Ixo	OH	As, Afr	
<i>Orthomyxoviridae</i>				
<i>Influenzavirus A</i>		PH	Worldwide	Avian influenza
<i>Paramyxoviridae: Paramyxovirus</i>				
Newcastle disease virus		PH	Worldwide	Newcastle disease
<i>Adenoviridae</i>				
<i>Aviadenovirus galli-1</i>		PH	Worldwide	Egg-drop syndrome
<i>Poxviridae</i>				
<i>Acipoxvirus</i>		PH	Worldwide	Avian pox
<i>Herpesviridae</i>				
<i>Herpesvirus anatis</i>		PH	Am, Eur	Duck plague
<i>Rickettsiales</i>				
<i>Rickettsia sibirica</i>	Ixo	OH, T	As	
<i>Coxiella burnetii</i>	(Ixo)	OH (T)	Worldwide	
<i>Anaplasma phagocytophilum</i>	Ixo	T, OH	Holarctic	
<i>Chlamydiaceae</i>				
<i>Chlamydophila psittaci</i>		PH	Worldwide	Ornithosis
<i>Mycoplasmataceae</i>				
<i>Mycoplasma gallisepticum</i>		OH	Am	Mycoplasmosis
<i>Spirochaetaceae</i>				
<i>Borrelia burgdorferi</i> s.l.	Ixo	OH, T	Holarctic	
<i>Campylobacteraceae</i>				
<i>Campylobacter jejuni</i>		PH	Worldwide	Campylobacteriosis
<i>Vibrionaceae</i>				
<i>Vibrio cholerae</i>		OH	Am	
<i>Enterobacteriaceae</i>				
<i>Escherichia coli</i> (enteropathogenic)		OH	Worldwide	Colibacillosis
<i>Salmonella enterica</i>		OH	Worldwide	Salmonellosis
<i>Yersinia enterocolitica</i>		OH	Eur, As	
<i>Y. pseudotuberculosis</i>		OH	Worldwide	Pseudotuberculosis
<i>Pasteurellaceae</i>				
<i>Pasteurella multocida</i>		PH	Worldwide	Avian cholera
<i>Riemerella anatipestifer</i>		PH	Worldwide	New duck disease

TABLE 1. Continued.

Agent	Vector ^a	Association ^b	Distribution ^c	Avian disease
Gram-positive cocci				
<i>Staphylococcus aureus</i>		OH	Worldwide	Staphylococcosis
<i>Enterococcus faecalis</i>		OH	Eur	
Endospore-forming gram-positive rods				
<i>Clostridium botulinum</i>		OH	Worldwide	Avian botulism
<i>C. perfringens</i>		OH	Worldwide	Necrotic enteritis
Regular nonsporing gram-positive rods				
<i>Listeria monocytogenes</i>		OH	Eur, As	Listeriosis
<i>Erysipelothrix rhusiopathiae</i>		OH	Am, As	Erysipelas
<i>Mycobacteriaceae</i>				
<i>Mycobacterium avium</i>		PH	Worldwide	Avian tuberculosis
<i>Endomycetes</i>				
<i>Candida albicans</i>		OH	Worldwide	Candidosis
<i>C. tropicalis</i>		OH	Worldwide	
<i>Hyphomycetes</i>				
<i>Aspergillus fumigatus</i>		OH	Worldwide	Aspergillosis
<i>Piroplasmida</i>				
<i>Babesia microti</i>	Ixo	T	Holarctic	
<i>Haemosporina</i>				
<i>Plasmodium</i> spp.	Cul	PH	Worldwide	Avian malaria
<i>Leucocytozoon simondi</i>	Sim	PH	Holarctic	Leucocytozoonosis
<i>Haemoproteus</i> spp.	Dip	PH	Worldwide	Hemoproteosis
<i>Eimeriina</i>				
<i>Toxoplasma gondii</i>		OH	Worldwide	Toxoplasmosis
<i>Eimeria</i> spp.		PH	Worldwide	Coccidiosis
<i>Sarcocystis</i> spp.		PH	Worldwide	Sarcosporidiosis
<i>Cryptosporidium</i> spp.		OH	Worldwide	Cryptosporidiosis
<i>Kinetoplastida</i>				
<i>Trypanosoma avium</i>	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*, *Vanel-lus vanellus*, and *Sturnus vulgaris* in Slo-vakia (during spring migration; Ernek et al., 1973, 1977); and migrating birds in Es-tonia (Uryvaev et al., 1992). It is most probable that the causative agent of Ock-elbo disease ("Pogosta," "Karelian fever"; i.e., Sindbis virus) was introduced to Fen-noscandia from subtropical regions by mi-gratory birds (Hubálek, 1994).

Eastern and western equine encephalitis viruses (mosquitoborne): Repeatedly iso-lated 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-migrat-ing birds (*Colaptes auratus*, *Icterus gal-bula*, *Zonotrichia albicollis*) in eastern Long Island (New York, USA); the mi-grants were thought responsible for initi-ating 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 och-*

ropus, *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 migra-

tory 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 mosquito-borne *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).

Tyuleni 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 (mosquito-borne): 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, mi-

gratory 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 spirochete 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 borreliæ (*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 feed-stuffs 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 (*Phoenicoptrus 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 (Gołebowski, 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; Husong 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 nonsporng 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 epornitits (*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 Trembl, 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 mosquito-borne 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 occasionally result in fatalities. These parasites are distributed by migratory waterfowl (Nation and Wobeser, 1977; Gajadhar et al., 1983; Wobeser, 1997). Other coccidia, *E. aythiae*, *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 hippoboscids flies, black-flies, or biting midges (Hubálek, 1994).

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LITERATURE CITED

- ALEKSEEV, A. N., AND H. V. DUBININA. 2003. Multiple infections of tick-borne pathogens in *Ixodes* spp. (Acarina: Ixodidae). *Acta Zoologica Lithuanica* 13: 311–321.
- , A. V. SEMENOV, AND C. V. BOLSHAKOV. 2001. Evidence of ehrlichiosis agents found in ticks (Acari: Ixodidae) collected from migratory birds. *Journal of Medical Entomology* 38: 471–474.
- ALEXANDER, D. J. 2000. A review of avian influenza in different bird species. *Veterinary Microbiology* 74: 3–13.
- ANDERSON, J. F., T. G. ANDREADIS, C. R. VOSSBRINCK, S. TIRRELL, E. M. WAKEM, R. A. FRENCH, A. E. GARMENDIA, AND H. J. VAN KRUNINGEN. 1999. Isolation of West Nile virus from mosquitoes, crows, and a Cooper's Hawk in Connecticut. *Science* 286: 2331–2333.
- ANDERSON, J. F., AND L. A. MAGNARELLI. 1984. Avian and mammalian hosts for spirochete-infected ticks and insects in a Lyme disease focus in Connecticut. *Yale Journal of Biology and Medicine* 57: 627–641.
- ANKERBERG, C. W. 1984. Pelican deaths in the vicinity of a sewage lift station: A bacteriological investigation. *Microbios Letters* 26: 33–42.
- BAHL, A. K., B. S. POMEROY, S. MANGUNDIMEDJO, AND B. C. EASTERDAY. 1977. Isolation of type A influenza and Newcastle disease viruses from migratory waterfowl in the Mississippi flyway. *Journal of the American Veterinary Medicine Association* 171: 949–951.
- BAST, T. F., S. WHITNEY, AND J. L. BENACH. 1973. Consideration on the ecology of several arboviruses in eastern Long Island. *American Journal of Tropical Medicine and Hygiene* 22: 109–115.
- BEER, J. V. 1963. The incidence of *Aspergillus fumigatus* in the throats of wild geese and gulls. *Sabouraudia* 2: 238–247.
- BENNETT, G. F. 1993. Phylogenetic distribution and possible evolution of the species of the Haemoproteidae. *Systematic Parasitology* 26: 39–44.
- , W. BLANDIN, H. W. HEUSMANN, AND A. G. CAMPBELL. 1974. Hematozoa of the Anatidae of the Atlantic flyway, I. Massachusetts. *Journal of Wildlife Diseases* 10: 442–451.
- , A. D. SMITH, W. WHITMAN, AND M. CAMERON. 1975. Hematozoa of the Anatidae of the Atlantic flyway, II. The maritime provinces of Canada. *Journal of Wildlife Diseases* 11: 280–289.
- BENSCH, A., AND S. AKESSON. 2003. Temporal and spatial variation of hematozoans in Scandinavian willow warblers. *Journal of Parasitology* 89: 388–391.
- BERNARD, K. A., J. G. MAFFEI, S. A. JONES, E. B. KAUFFMAN, AND G. D. EBEL. 2001. West Nile virus infection in birds and mosquitoes, New York State, 2000. *Emerging Infectious Diseases* 7: 679–685.
- BJOERSDORF, A., S. BERGSTROM, R. F. MASSUNG, P. D. HAEMIG, AND B. OLSEN. 2001. *Ehrlichia*-infected ticks on migrating birds. *Emerging Infectious Diseases* 7: 877–879.
- BOLTE, A. L., J. MEURER, AND E. F. KALETA. 1999. Avian host spectrum of avipoxviruses. *Avian Pathology* 28: 415–432.
- BOUTTEFROY, A., J. P. LEMAITRE, AND A. ROUSSET. 1997. Prevalence of *Listeria* sp. in droppings from urban rooks (*Corvus frugilegus*). *Journal of Applied Microbiology* 82: 641–647.
- BOYLE, D. B., R. W. DICKERMAN, AND I. D. MARSHALL. 1983. Primary viraemia responses of herons to experimental infection with Murray Valley encephalitis, Kunjin and Japanese encephalitis viruses. *Australian Journal of Experimental Biology and Medical Sciences* 61: 655–664.
- BRADBURY, J. M., A. VUILLAUME, J. P. DUPIELLET, M. FORREST, J. L. BIND, AND G. GAILLARD-PERRIN. 1987. Isolation of *Mycoplasma cloacale* from a number of different avian hosts in Great Britain and France. *Avian Pathology* 16: 183–186.
- BRAND, C. J. 1984. Avian cholera in the Central and Mississippi Flyways during 1979–80. *Journal of Wildlife Management* 48: 399–406.
- . 1989. Chlamydial infections in free-living birds. *Journal of American Veterinary Medical Association* 195: 1531–1535.
- BRINCK, P., A. SVEDMYR, AND G. VON ZEIPPEL. 1965. Migrating birds at Ottenby, Sweden, as carriers of ticks and possible transmitters of tick-borne encephalitis virus. *Oikos* 16: 88–99.
- BROMAN, T., H. PALMGREN, S. BERGSTRÖM, M. SELIN, J. WALDENSTRÖM, M.-L. DANIELSSON-THAM, AND B. OLSEN. 2002. *Campylobacter jejuni* in black-headed gulls (*Larus ridibundus*): prevalence, genotypes, and influence on *C. jejuni* epidemiology. *Journal of Clinical Microbiology* 40: 4594–4602.
- BUCK, J. D. 1983. Occurrence of *Candida albicans* in fresh gull feces in temperate and subtropical areas. *Microbial Ecology* 9: 171–176.
- . 1986. A note on the experimental uptake and clearance of *Candida albicans* in a young captive gull (*Larus* sp.). *Mycopathologia* 94: 59–61.
- . 1990. Isolation of *Candida albicans* and halophilic *Vibrio* spp. from aquatic birds in Connecticut and Florida. *Applied and Environmental Microbiology* 56: 826–828.

- BUESCHER, E. L., W. F. SCHERER, H. E. MCCLURE, J. T. MOYER, M. Z. ROSENBERG, M. YOSHI, AND Y. OKADA. 1959. Ecologic studies of Japanese encephalitis virus in Japan. *Avian infection. American Journal of Tropical Medicine and Hygiene* 8: 678–688.
- BURGESS, E. C. 1989. Experimental inoculation of mallard ducks (*Anas platyrhynchos platyrhynchos*) with *Borrelia burgdorferi*. *Journal of Wildlife Diseases* 94: 99–102.
- CALISHER, C. H., K. S. C. MANESS, R. D. LORD, AND P. H. COLEMAN. 1971. Identification of two South American strains of eastern equine encephalomyelitis virus from migrant birds captured on the Mississippi delta. *American Journal of Epidemiology* 94: 172–178.
- , E. GUTIÉRREZ, K. S. C. MANESS, AND R. D. LORD. 1974. Isolation of Mayaro virus from a migrating bird captured in Louisiana in 1967. *Boletino Office Sanitaria Pan-American* 8: 243–248.
- , N. KARABATSOS, AND A. R. FILIPE. 1987. Antigenic uniformity of toptotype strains of Thogoto virus from Africa, Europe, and Asia. *American Journal of Tropical Medicine and Hygiene* 37: 670–673.
- , T. G. SCHWAN, J. S. LAZUICK, R. B. EADS, AND D. B. FRANCY. 1988. Isolation of Mono Lake virus (family Reoviridae, genus Orbivirus, Kemerovo serogroup) from *Argas cooleyi* (Acari: Argasidae) collected in Colorado. *Journal of Medical Entomology* 25: 388–390.
- ČERNÝ, V., AND F. BALÁT. 1957. A case of introduction of *Hyalomma marginatum* ticks to Czechoslovakia. *Zoologické Listy* 6: 81–83. [In Czech.]
- CHASTEL, C. E. 1988. Tick-borne virus infections of marine birds. *Advances in Disease Vector Research* 5: 25–60.
- CONVERSE, J. D., H. H. HOOGSTRAAL, M. I. MOUSSA, M. STEK, AND M. N. KAISER. 1974. Bahig virus (Tete group) in naturally- and transovarially-infected *Hyalomma marginatum* ticks from Egypt and Italy. *Archiv für die gesamte Virusforschung* 46: 29–35.
- COOPER, J. E. 1990. Birds and zoonoses. *Ibis* 132: 181–191.
- COULSON, J. C., J. BUTTERFIELD, AND C. THOMAS. 1983. The herring gull *Larus argentatus* as a likely transmitting agent of *Salmonella montevideo* to sheep and cattle. *Journal of Hygiene* 91: 437–444.
- CRAGG, J., AND Y. M. CLAYTON. 1971. Bacterial and fungal flora of seagull droppings in Jersey. *Journal of Clinical Pathology* 24: 317–319.
- DANIELS, T. J., G. R. BATTALY, D. LIVERIS, R. C. FALCO, AND I. SCHWARTZ. 2002. Avian reservoirs of the agent of human granulocytic ehrlichiosis? *Emerging Infectious Diseases* 8: 1524–1525.
- DAVIS, J. W., R. C. ANDERSON, L. KARSTAD, AND D. O. TRAINER. 1971. Infectious and parasitic diseases of wild birds. Iowa State University Press, Ames, Iowa, 344 pp.
- DE MARCO, M. A., G. E. FONI, L. CAMPITELLI, E. RAFFINI, L. DI TRANI, M. DELOGU, V. GUBERTI, G. BARIGAZZI, AND I. DONATELLI. 2003. Circulation of influenza viruses in wild waterfowl wintering in Italy during 1993–99 periods: Evidence of virus shedding and seroconversion in wild ducks. *Avian Diseases* 47: 861–866.
- DICKERMAN, R. W., M. S. MARTIN, AND E. A. DI-PAOLA. 1980. Studies on Venezuelan encephalitis in migrating birds in relation to possible transport of virus from South to Central America. *American Journal of Tropical Medicine and Health* 29: 269–276.
- DOHERTY, R. L., J. G. CARLEY, M. D. MURRAY, A. J. MAIN, B. H. KAY, AND R. DOMROW. 1975. Isolation of arboviruses (Kemerovo group, Sakhalin group) from *Ixodes uriae* collected at Macquarie Island, Southern Ocean. *American Journal of Tropical Medicine and Hygiene* 24: 521–526.
- DUPUIS, A. P., P. P. MARRA, AND L. D. KRAMER. 2003. Serologic evidence of West Nile virus transmission, Jamaica, West Indies. *Emerging Infectious Diseases* 9: 860–863.
- ECCLES, M. A. 1939. The role of birds in the spread of foot-and-mouth disease. *Bulletin de l'Office International de Epizootiques* 18: 118–148.
- ERNEK, E., O. KOUCH, M. GREŠÍKOVÁ, J. NOSEK, AND M. SEKEYOVÁ. 1973. Isolation of Sindbis virus from the reed warbler (*Acrocephalus scirpaceus*) in Slovakia. *Acta Virologica* 17: 359–361.
- , M. LICHARD, AND J. NOSEK. 1968. The role of birds in the circulation of tick-borne encephalitis virus in the Tribeč region. *Acta Virologica* 12: 468–470.
- , J. NOSEK, J. TEPLAN, AND Č. FOLK. 1977. Arboviruses in birds captured in Slovakia. *Journal of Hygiene, Epidemiology, Microbiology and Immunology* 21: 353–359.
- FENLON, D. R. 1981. Seagulls (*Larus* spp.) as vectors of salmonellae: An investigation into the range of serotypes and numbers of salmonellae in gull faeces. *Journal of Hygiene* 86: 195–202.
- . 1985. Wild birds and silage as reservoirs of *Listeria* in the agricultural environment. *Journal of Applied Bacteriology* 59: 537–543.
- FILIPE, A. R., AND J. CASALS. 1979. Isolation of Dhori virus from *Hyalomma marginatum* ticks in Portugal. *Intervirology* 11: 124–127.
- FOUCHIER, R. A., B. OLSEN, T. M. BESTEBROER, S. HERFST, L. VAN DER KEMP, G. F. RIMMELZWAAN, AND A. D. M. E. OSTERHAUS. 2003. Influenza A virus surveillance in wild birds in northern Europe in 1999 and 2000. *Avian Diseases* 47: 857–860.
- FUKUSHIMA, H., AND M. GOMYODA. 1991. Intestinal carriage of *Yersinia pseudotuberculosis* by wild birds and mammals in Japan. *Applied and Environmental Microbiology* 57: 1152–1155.

- GAIDAMOVICH, S. Y., L. P. NIKIFOROV, V. L. GROMASHEVSKI, N. M. MIRZOEVA, V. I. CHERVONSKI, AND N. V. KHUTORETSKAYA. 1968. Isolation of group A and B arboviruses in Azerbaijan. Materialy XV Nauchnoi Sessii Instituta Poliomiellita i Virusnykh Encefalitov (Moskva) 3: 185–186. [In Russian.]
- GAJADHAR, A. A., G. WOBESER, AND P. H. G. STOCKDALE. 1983. Coccidia of domestic and wild waterfowl (Anseriformes). Canadian Journal of Zoology 61: 1–24.
- GARMENDIA, A. E., H. J. VAN KRUININGEN, R. A. FRENCH, J. F. ANDERSON, T. G. ANDREADIS, A. KUMAR, AND A. B. WEST. 2000. Recovery and identification of West Nile virus from a hawk in winter. Journal of Clinical Microbiology 38: 3110–3111.
- GERN, L., AND O. RAIS. 1996. Efficient transmission of *Borrelia burgdorferi* between cofeeding *Ixodes ricinus* ticks (Acari: Ixodidae). Journal of Medical Entomology 33: 189–192.
- GLÜNDER, G. 1989. Charakterisierung von *Campylobacter* spp. aus Wildvögeln. Berliner-Münchener Tierärztliche Wochenschrift 102: 49–52.
- , AND S. PETERMANN. 1989. Vorkommen und Charakterisierung von *Campylobacter* spp. bei Silbermöwen (*Larus argentatus*), Dreizehnmöwen (*Rissa tridactyla*) und Haussperlingen (*Passer domesticus*). Journal of Veterinary Medicine B 36: 123–130.
- , U. NEUMANN, AND S. BRAUNE. 1992. Occurrence of *Campylobacter* spp. in young gulls, duration of campylobacter infection and reinfection by contact. Journal of Veterinary Medicine B 39: 119–122.
- GOLBIEWSKI, S. 1975. The carriage of pathogenic bacteria in free-living birds. Medycyna Weterynarna 31: 143–144. [In Polish.]
- GORDEEVA, Z. E. 1980. Ecological connections between arboviruses and wild birds in Tajikistan. In Ecology of viruses, D. K. Lvov (ed.). Institute of Virology, Moskva, pp. 126–130. [In Russian.]
- GRACZYK, T. K., R. FAYER, J. M. TROUT, E. J. LEWIS, C. A. FARLEY, I. SULAIMAN, AND A. A. LAL. 1998. *Giardia* sp. cysts and infectious *Cryptosporidium parvum* oocysts in the feces of migratory Canada geese (*Branta canadensis*). Applied and Environmental Microbiology 64: 2736–2738.
- GRIMES, J. E., K. J. OWENS, AND J. R. SINGER. 1979. Experimental transmission of *Chlamydia psittaci* to turkeys from wild birds. Avian Diseases 24: 915–926.
- GRUSON, E. S. 1976. Checklist of the birds of the world. Collins, London, UK, 212 pp.
- GULKA, C. M., T. H. PIELA, V. J. YATES, AND C. BAGSHAW. 1984. Evidence of exposure of waterfowl and other aquatic birds to the hemagglutinating duck adenovirus identical to EDS-76 virus. Journal of Wildlife Diseases 20: 1–5.
- GYLFE, A., B. OLSÉN, D. STRASEVICIUS, N. M. RAS, P. WEIHE, L. NOPPA, Z. OSTBERG, G. BARANTON, AND S. BERGSTRÖM. 1999. Isolation of Lyme disease *Borrelia* from puffins (*Fratricula arctica*) and seabird ticks (*Ixodes uriae*) on the Faeroe Islands. Journal of Clinical Microbiology 37: 890–896.
- , S. BERGSTRÖM, J. LUNDSTRÖM, AND B. OLSÉN. 2000. Reactivation of *Borrelia* infection in birds. Nature 403: 724–725.
- HABERKORN, A. 1968. Zur hormonellen Beeinflussung von *Haemoproteus*-Infektionen. Zeitschrift für Parasitenkunde 31: 108–112.
- HÁJEK, V., J. BALUSEK, V. HORÁK, AND D. KOUKALOVÁ. 1991. Characterization of coagulase-positive staphylococci isolated from free-living birds. Journal of Hygiene, Epidemiology, Microbiology and Immunology 35: 407–418.
- HAMASAKI, S.-I., H. HAYASHIDANI, K.-I. KANEKO, M. PGAWA, AND Y. SHIGETA. 1989. A survey for *Yersinia pseudotuberculosis* in migratory birds in coastal Japan. Journal of Wildlife Diseases 25: 401–403.
- HANINCOVÁ, K., V. TARAGELOVÁ, J. KOCI, S. M. SCHÄFER, R. HAILS, A. J. ULLMANN, J. PIESMAN, M. LABUDA, AND K. KURTENBACH. 2003. Association of *Borrelia garinii* and *B. valaisiana* with songbirds in Slovakia. Applied and Environmental Microbiology 69: 2825–2830.
- HANNOUN, C., B. CORNIU, AND J. MOUCHET. 1972. Role of migrating birds in arbovirus transfer between Africa and Europe. In Transcontinental connections of migratory birds and their role in the distribution of arboviruses, A. I. Cherepanov (ed.). Nauka, Novosibirsk, Russia, pp. 167–172.
- HARTUP, B. K., A. A. DHONDT, K. V. SYDENSTRICKER, W. M., HOCHACHKA, AND G. V. KOLLAS. 2001. Host range and dynamics of mycoplasmal conjunctivitis among birds in North America. Journal of Wildlife Diseases 37: 72–81.
- HASLETT, T. M., AND W. J. SCHNEIDER. 1978. Occurrence and attempted transmission of *Toxoplasma gondii* in European starlings (*Sturnus vulgaris*). Journal of Wildlife Diseases 14: 173–175.
- HEJLÍČEK, K., AND F. TREML. 1993. The occurrence of avian mycobacteriosis in free-living birds at different epizootiological situation of poultry tuberculosis. Veterinární Medicína 38: 305–317. [In Czech.]
- HERNANDEZ, J., J. BONNEDAHN, J. WALDENSTRÖM, H. PALMGREN, AND B. OLSEN. 2003. *Salmonella* in birds migrating through Sweden. Emerging Infectious Diseases 9: 753–755.
- HILL, H. M., AND L. M. GRAHAM. 1961. Waterfowl botulism outbreak in San Joacinto Valley, Riverside county, California. California Fish and Game 47: 113–114.
- HINSHAW, V. S., AND R. G. WEBSTER. 1982. The natural history of influenza A viruses. In Basic and

- applied influenza research, A. S. Beare (ed.). CRC Press, Boca Raton, pp. 79–104.
- , AND B. TURNER. 1980. The perpetuation of orthomyxoviruses and paramyxoviruses in Canadian waterfowl. *Canadian Journal of Microbiology* 26: 622–629.
- , G. M. WOOD, R. G. WEBSTER, R. DEIBEL, AND B. TERNER. 1985. Circulation of influenza viruses and paramyxoviruses in waterfowl: Comparison of different migratory flyways in North America. *Bulletin of the World Health Organisation* 63: 711–719.
- HINZ, K. H., M. RYLL, B. KÖHLER, AND G. GLÜNDER. 1998. Phenotypic characteristics of *Riemerella anatipestifer* and similar micro-organisms from various hosts. *Avian Pathology* 27: 33–42.
- HOOGSTRAAL, H. 1976. Viruses and ticks from migrating birds. In *Naturherde von Infektionskrankheiten in Zentraleuropa*, W. Sixl and H. Troger (eds.). University Press, Graz, Austria, pp. 27–50.
- . 1979. The epidemiology of tick-borne Crimean-Congo hemorrhagic fever in Asia, Europe and Africa. *Journal of Medical Entomology* 15: 307–417.
- , M. N. KAISER, M. A. TRAYLOR, S. GABER, AND E. GUINDY. 1961. Ticks (Ixodoidea) on birds migrating from Africa to Europe and Asia. *Bulletin of the World Health Organisation* 24: 197–212.
- , ———, ———, E. GUINDY, AND S. GABER. 1963. Ticks (Ixodidae) on birds migrating from Europe and Asia to Africa, 1959–1961. *Bulletin of the World Health Organisation* 28: 235–262.
- , M. A. TRAYLOR, S. GABER, G. MALAKATIS, E. GUINDY, AND I. HELMY. 1964. Ticks (Ixodidae) on migrating birds in Egypt, spring and fall 1962. *Bulletin of the World Health Organisation* 30: 355–367.
- HUBÁLEK, Z. 1994. Pathogenic microorganisms associated with free-living birds (a review). *Acta Scientiarum Naturalium Brno* 28: 1–74.
- , V. ČERNÝ, AND P. RÖDL. 1982. Possible role of birds and ticks in the dissemination of Bhanja virus. *Folia Parasitologica* 29: 85–95.
- , J. F. ANDERSON, J. HALOUZKA, AND V. HÁJEK. 1996. Borreliae in immature *Ixodes ricinus* (Acari: Ixodidae) ticks parasitizing birds in the Czech Republic. *Journal of Medical Entomology* 33: 766–771.
- HUMAIR, P. F., N. TURRIAN, A. AESCHLIMANN, AND L. GERN. 1993. *Ixodes ricinus* immatures on birds in a focus of Lyme borreliosis. *Folia Parasitologica* 40: 237–242.
- HUNTER, B., AND G. WOBESER. 1980. Pathology of experimental avian cholera in mallard ducks (*Anas platyrhynchos*). *Avian Diseases* 24: 403–414.
- HURST, G. W. 1968. Foot-and-mouth disease. The possibility of continental sources of the virus in England in epidemics of October 1967 and several other years. *The Veterinary Record* 82: 610–614.
- HUSSONG, D., J. M. DAMARÉ, R. J. LIMPET, W. J. L. SLADEN, R. M. WEINER, AND R. COLWELL. 1979. Microbial impact of Canada geese (*Branta canadensis*) and whistling swans (*Cygnus columbianus columbianus*) on aquatic ecosystems. *Applied and Environmental Microbiology* 37: 14–20.
- JENSEN, W. I., AND S. I. COTTER. 1976. An outbreak of erysipelas in eared grebes (*Podiceps nigricollis*). *Journal of Wildlife Diseases* 12: 583–586.
- KAISER, M. N., H. HOOGSTRAAL, AND G. E. WATSON. 1974. Ticks (Ixodoidea) on migrating birds in Cyprus, fall 1967 and spring 1968, and epidemiological considerations. *Bulletin of Entomological Research* 64: 97–110.
- KALETA, E. F. 2002. Foot-and-mouth disease: Susceptibility of domestic poultry and free-living birds to infection and to disease. *Deutsche Tierärztliche Wochenschrift* 109: 391–399.
- , AND E. M. A. TADAY. 2003. Avian host range of *Chlamydophila* spp. based on isolation, antigen detection and serology. *Avian Pathology* 32: 435–462.
- , S. E. D. KHALAF, AND O. SIEGMANN. 1980. Antibodies to egg-drop syndrome 76 virus in wild birds in possible conjunction with egg-shell problems. *Avian Pathology* 9: 587–590.
- KANAI, H., H. HASHIMOTO, AND S. MITSUHASHI. 1981. Drug-resistance and conjugative R plasmids in *Escherichia coli* strains isolated from wild birds (Japanese tree sparrows, green pheasants and bamboo partridges). *Japanese Poultry Science* 18: 234–239.
- KANEUCHI, C., M. SHIBATA, T. KAWASAKI, T. KARIU, M. KANZAKI, AND T. MARUYAMA. 1989. Occurrence of *Yersinia* spp. in migratory birds, ducks, and swallows in Japan. *Japanese Journal of Veterinary Science* 51: 805–808.
- KAPPERUD, G., AND O. ROSEF. 1983. Avian wildlife reservoir of *Campylobacter fetus* ssp. *jejuni*, *Yersinia* spp. and *Salmonella* spp. in Norway. *Applied and Environmental Microbiology* 45: 375–380.
- KATO, Y., K. ITO, Y. KUBOKURA, T. MARUYAMA, K.-I. KANEKO, AND M. OGAWA. 1985. Occurrence of *Yersinia enterocolitica* in wild living birds and Japanese serows. *Applied and Environmental Microbiology* 49: 198–200.
- KAWAKITA, S., AND N. VAN UDEN. 1965. Occurrence and population densities of yeast species in the digestive tracts of gulls and terns. *Journal of General Microbiology* 39: 125–129.
- KAWAOKA, Y., K. OTSUKI, T. MITANI, T. KUBOTA, AND M. TSUBOKURA. 1984. Migratory waterfowl as flying reservoirs of *Yersinia* species. *Research in Veterinary Science* 37: 266–268.
- KEMPF, I., C. CHASTEL, S. FERRIS, F. GESBERT, AND

- A. BLANCHARD. 2000. Isolation and characterisation of a mycoplasma from a kittiwake (*Rissa tridactyla*). *Veterinary Record* 146: 168.
- KEYMER, I. F. 1958. A survey and review of the causes of mortality in British birds and the significance of wild birds as disseminators of disease. *Veterinary Record* 70: 713–720, 736–740.
- KOMAR, N., R. LANCIOTTI, R. BOWEN, S. LANGEVIN, AND M. BUNNING. 2002. Detection of West Nile virus in oral and cloacal swabs collected from bird carcasses. *Emerging Infectious Diseases* 8: 741–742.
- , S. LANGEVIN, S. HINTEN, N. NEMETH, E. EDWARDS, D. HETTLER, B. DAVIS, R. BOWEN, AND M. BUNNING. 2003a. Experimental infection of North American birds with the New York 1999 strain of West Nile virus. *Emerging Infectious Diseases* 9: 311–322.
- KOMAR, O., M. B. ROBBINS, K. KLENK, B. J. BLITVICH, N. L. MARLENEE, K. L. BURKHALTER, D. J. GUBLER, G. GONZÁLVES, C. J. PENA, A. T. PETERSON, AND N. KOMAR. 2003b. West Nile virus transmission in resident birds, Dominican Republic. *Emerging Infectious Diseases* 9: 1299–1302.
- LEE, J. V., D. J. BASHFORD, AND T. J. DONOVAN. 1982. The incidence of *Vibrio cholerae* in water, animals and birds in Kent, England. *Journal of Applied Bacteriology* 52: 281–291.
- LITERÁK, I., K. HEJLIČEK, J. NEZVAL, AND Č. FOLK. 1992. Incidence of *Toxoplasma gondii* in populations of wild birds in the Czech Republic. *Avian Pathology* 21: 659–665.
- LORD, R. D., AND C. H. CALISHER. 1970. Further evidence of southward transport of arboviruses by migratory birds. *American Journal of Epidemiology* 92: 73–78.
- LUECHTEFELD, N. A., M. J. BLASER, L. B. RELLER, AND W. L. WANG. 1980. Isolation of *Campylobacter fetus* subsp. *jejuni* from migratory waterfowl. *Journal of Clinical Microbiology* 12: 406–408.
- LVOV, D. K., AND V. D. ILICHEV. 1979. Avian migrations and transport of infection agents. Nauka, Moskva, 270 pp. [In Russian.]
- , A. A. TIMOPHEEVA, V. A. SMIRNOV, V. L. GROMASHEVSKY, G. A. SIDOROVA, L. P. NIKIFOROV, A. A. SAZONOV, A. P. ANDREEV, T. M. SKVORTZOVA, L. K. BEREZINA, AND V. A. ARISTOVA. 1975. Ecology of tick-borne viruses in colonies of birds in the USSR. *Medical Biology* 53: 325–330.
- MACDONALD, J. W. 1968. Listeriosis and erysipelas in wild birds. *Bird Study* 15: 37–38.
- , D. OWEN, K. G. SPENCER, AND P. E. CURTIS. 1981. Pasteurellosis in wild birds. *The Veterinary Record* 109: 58.
- MAGNARELLI, L. A., K. C. STAFFORD, AND V. C. BLADEN. 1992. *Borrelia burgdorferi* and *Ixodes dammini* (Acari: Ixodidae) feeding on birds in Lyme, Connecticut, U.S.A. *Canadian Journal of Zoology* 70: 2322–2325.
- MAIN, A. J., W. G. DOWNS, R. E. SHOPE, AND R. C. WALLIS. 1973. Great Island and Bauline: Two new Kemerovo group orbiviruses from *Ixodes uriae* in eastern Canada. *Journal of Medical Entomology* 10: 229–235.
- , ———, ———, AND ———. 1976. Avalon and Clo Mor: Two new Sakhalin group viruses from the North Atlantic. *Journal of Medical Entomology* 13: 309–315.
- MALE, T. 2003. Potential impact of West Nile virus on American avifaunas. *Conservation Biology* 17: 928–930.
- MALKINSON, M., AND Y. WEISMAN. 1980. Serological survey for the prevalence of antibodies to egg-drop syndrome 1976 virus in domesticated and wild birds in Israel. *Avian Pathology* 9: 421–426.
- , C. BANET, Y. WEISMAN, S. POKAMUNSKI, R. KING, M.-T. DROUET, AND V. DEUBEL. 2002. Introduction of West Nile virus in the Middle East by migrating white storks. *Emerging Infectious Diseases* 8: 392–397.
- MATHIS, C., AND M. LEGER. 1910. Leucocytozoon d'une tourterelle (*Turtur humilis*) et d'une sarcelle (*Querquedula crecca*) du Tonkin. *Compte Rendu de la Societe Biologique* 68: 118–120.
- MATUKHIN, V. N., AND T. N. FEDOROVA. 1969. Serological investigations of birds to some viruses of tick-borne encephalitis complex. In *Pereletnye pticy i ich rol v rasprostraneni arbovirusov*, A. I. Cherepanov (ed.). Nauka, Novosibirsk, pp. 287–293. [In Russian.]
- MATVEEV, K. I., AND N. D. KONSTANTINOVA. 1974. The role of migratory birds in the spread of *Clostridium botulinum*. *Gigiena i Sanitaria* 12: 91–92. [In Russian.]
- MCDIARMID, A. 1969. Diseases in free-living wild animals. Academic Press, London, UK, 332 pp.
- MONATH, T. P., J. S. LAZUICK, C. B. CROPP, W. A. RUSH, C. H. CALISHER, R. M. KINNEY, D. W. TRENT, G. E. KEMP, G. S. BOWEN, AND D. B. FRANCY. 1980. Recovery of Tonate virus ('Bijou Bridge' strain), a member of the Venezuelan equine encephalomyelitis virus complex, from cliff swallow nest bugs (*Oeciacus vicarius*) and nestling birds in North America. *American Journal of Tropical Medicine and Hygiene* 29: 969–983.
- MORRIS, C. D., E. WHITNEY, T. F. BAST, AND R. DEIBEL. 1973. An outbreak of eastern equine encephalomyelitis in upstate New York during 1971. *American Journal of Tropical Medicine and Hygiene* 22: 561–566.
- NATION, P. N., AND G. WOBESER. 1977. Renal coccidiosis in wild ducks in Saskatchewan. *Journal of Wildlife Diseases* 13: 370–375.
- NIR, Y., R. GOLDWASSER, Y. LASOWSKI, AND A. AVIVI. 1967. Isolation of arboviruses from wild birds in

- Israel. American Journal of Epidemiology 86: 372–378.
- NISKANEN, T., J. WALDENSTRÖM, M. FREDRIKSSON-AHOMAA, B. OLSEN, AND H. KORKEALA. 2003. *virF*-Positive *Yersinia pseudotuberculosis* and *Yersinia enterocolitica* found in migratory birds in Sweden. Applied and Environmental Microbiology 69: 4670–4675.
- NOSEK, J., AND Č. FOLK. 1977. Relationships of birds to arboviruses and their vectors. Acta Scientiarum Naturalium Brno 10(9): 1–61.
- NUORTEVA, P., AND H. HOOGSTRAAL. 1963. The incidence of ticks (Ixodoidea, Ixodidae) on migratory birds arriving in Finland during the spring of 1962. Annales Medicine Experimentale Fennici 41: 457–468.
- NUTTALL, P. A. 1997. Viruses, bacteria, and fungi of birds. In Host-parasite evolution, D. H. Clayton and J. Moore (eds.). University Press, Oxford, UK, pp. 271–302.
- , T. C. KELLY, D. CAREY, S. R. MOSS, AND K. A. HARRAP. 1984. Mixed infections with tick-borne viruses in a seabird colony in Eire. Archives of Virology 79: 35–44.
- , D. CAREY, S. R. MOSS, B. M. GREEN, AND R. P. SPENCE. 1986. Hughes group viruses (Bunyaviridae) from the seabird tick *Ixodes (Ceraticodes) uriae* (Acari: Ixodidae). Journal of Medical Entomology 23: 437–440.
- OGG, J. E., R. A. RYDER, AND H. L. SMITH. 1989. Isolation of *Vibrio cholerae* from aquatic birds in Colorado and Utah. Applied and Environmental Microbiology 55: 95–99.
- OLSEN, B., D. C. DUFFY, L. NOPPA, J. BUNIKIS, AND S. BERGSTRÖM. 1993. A Lyme borreliosis cycle in seabirds and *Ixodes uriae* ticks. Nature 362: 340–342.
- , ———, T. G. T. JAENSON, A. GYLFE, J. BONNEDAHN, AND S. BERGSTRÖM. 1995a. Transhemispheric exchange of Lyme disease spirochetes by seabirds. Journal of Clinical Microbiology 33: 3270–3274.
- , T. G. T. JAENSON, AND S. BERGSTRÖM. 1995b. Prevalence of *Borrelia burgdorferi* sensu lato infected ticks on migrating birds. Applied and Environmental Microbiology 61: 3082–3087.
- PAGE, L. A. 1976. Observations on the involvement of wildlife in an epornitic of chlamydiosis in domestic turkeys. Journal of American Veterinary Medicine Association 169: 932.
- PAK, S. M. 1976. Toxoplasmosis in birds in Kazakhstan. Nauka, Alma-Ata, 78 pp. [In Russian.]
- PALMGREN, H., M. SELLIN, S. BERGSTRÖM, AND B. OLSEN. 1997. Enteropathogenic bacteria in migrating birds arriving in Sweden. Scandinavian Journal of Infectious Diseases 29: 565–568.
- PAVLÁSEK, I. 1993. *Larus ridibundus*, a new host of *Cryptosporidium baileyi*. Veterinární Medicína 38: 629–638. [In Czech.]
- PAVLOVSKY, J. N., AND K. N. TOKAREVICH. 1966. Birds and infectious pathology of man. Medicina, Leningrad, 227 pp. [In Russian.]
- PEIRCE, M. A., AND C. J. MEAD. 1984. Haematzoa of British birds. Journal of Natural History 18: 335–340.
- PETERMANN, S., G. GLÜNDER, U. HEFFELS-REDMANN, AND K.-H. HINZ. 1989. Untersuchungsbefunde an “krank” bzw. “tot” gefundenen Trottelummen (*Uria aalge*), Dreizehen- (*Rissa tridactyla*), Silber- (*Larus argentatus*) und Lachmöwen (*Larus ridibundus*) aus dem Bereich der Deutschen Bucht, 1982–1985. Deutsche Tierärztliche Wochenschrift 96: 271–277.
- QUESSY, S., AND S. MESSIER. 1992. Prevalence of *Salmonella* spp., *Campylobacter* spp. and *Listeria* spp. in ring-billed gulls (*Larus delawarensis*). Journal of Wildlife Diseases 28: 526–531.
- RAPPOLE, J. H., AND Z. HUBÁLEK. 2000. Migratory birds and West Nile virus. Journal of Applied Microbiology Supplement 94: 47–58.
- , S. R. DERRICKSON, AND Z. HUBÁLEK. 2000. Migratory birds and spread of West Nile virus in the Western Hemisphere. Emerging Infectious Diseases 6: 319–328.
- REFSUM, T., K. HANDELAND, D. L. BAGGESEN, G. HOLSTAD, AND G. KAPPERUD. 2002. Salmonellae in avian wildlife in Norway from 1969 to 2000. Applied and Environmental Microbiology 68: 5595–5599.
- ROSICKÝ, B. 1965. Types of animal movements and their influence on natural foci of diseases. In Theoretical questions of natural foci of diseases, B. Rosický and K. Heyberger (eds.). Publishing House of the Czechoslovak Academy of Sciences, Prague, Czechoslovakia, pp. 151–162.
- SACKS, J. J., L. SPENCER, L. M. BALDY, S. BERTA, C. M. PATTON, M. C. WHITE, W. J. BIGLER, AND J. J. WITTE. 1986. Epidemic campylobacteriosis associated with a community water supply. American Journal of Public Health 76: 424–429.
- SAMBYAL, D. S., AND K. K. BAXI. 1980. Bacterial flora of the respiratory tract of wild birds in Ludhiana (Punjab), India. Zentralblatt für Veterinär-Medizin B 27: 165–168.
- SCHERER, W. F., E. L. BUESCHER, AND H. E. MCCLURE. 1959. Ecologic studies of Japanese encephalitis virus in Japan. Avian factors. American Journal of Tropical Medicine and Hygiene 8: 689–697.
- SCHMIDT, J. R., AND R. E. SHOPE. 1971. Kemerovo virus from a migrating common redstart of Eurasia. Acta Virologica 15: 112.
- SCHWAN, T. G., M. L. HIGGINS, AND B. C. NELSON. 1983. *Hectopsylla psittaci*, a South American sticktight flea (Siphonaptera: Pulicidae), established in cliff swallow nests in California, USA. Journal of Medical Entomology 20: 690–692.
- , J. J. OPRANDY, AND A. J. MAIN. 1988. Mono Lake virus infecting *Argas* ticks (Acari: Argasidae) associated with California gulls breeding on

- islands in Mono Lake, California. *Journal of Medical Entomology* 25: 381–387.
- SELLIN, M., H. PALMGREN, T. BROMAN, S. BERGSTRÖM, AND B. OLSEN. 2000. Involving ornithologists in the surveillance of vancomycin-resistant enterococci. *Emerging Infectious Diseases* 6: 87–88.
- SHAH, K. V., H. N. JOHNSON, T. R. RAO, P. K. RAJAGOPALAN, AND B. S. LAMBA. 1960. Isolation of five strains of Sindbis virus in India. *Indian Journal of Medical Research* 48: 300–308.
- SHARMA, S. N., AND K. K. BAXI. 1980. Isolation of a velogenic strain of Newcastle disease virus from *Upupa epops* (hoopoe). *Zentralblatt für Veterinär-Medizin B* 27: 677–679.
- SHAYEGANI, M., W. B. STONE, AND I. DEFORGE. 1986. *Yersinia enterocolitica* and related species isolated from wildlife in New York state. *Applied and Environmental Microbiology* 52: 420–424.
- SIXL, W., R. KARPÍŠKOVÁ, Z. HUBÁLEK, J. HALOUZKA, M. MIKULÁŠKOVÁ, AND J. SALAVA. 1997. *Campylobacter* spp. and *Salmonella* spp. in black-headed gulls (*Larus ridibundus*). *Central European Journal of Public Health* 5: 24–26.
- SLEMONS, R. D., AND B. C. EASTERDAY. 1977. Type A influenza viruses in the feces of migratory waterfowl. *Journal of American Veterinary Medicine Association* 171: 947–948.
- , M. C. SHIELDCASTLE, L. D. HEYMAN, K. E. BEDNARIK, AND D. A. SENNE. 1991. Type A influenza viruses in waterfowl in Ohio and implications for domestic turkeys. *Avian Diseases* 35: 165–173.
- SMIT, T., A. EGER, J. HAAGSMA, AND T. BAKHUIZEN. 1987. Avian tuberculosis in wild birds in the Netherlands. *Journal of Wildlife Diseases* 23: 485–487.
- SMITH, H. V., J. BROWN, J. C. COULSON, G. P. MORRIS, AND R. W. A. GIRDWOOD. 1993. Occurrence of oocysts of *Cryptosporidium* sp. in *Larus* spp. gulls. *Epidemiology and Infection* 110: 135–143.
- SOMOV, G. P., AND G. M. SOLDATOV. 1964. On the role of birds in circulation of tick-borne spotted typhus in nature. *Zhurnal Mikrobiologii, Epidemiologii i Immunobiologii* 1: 126–129. [In Russian.]
- SPALDING, M. G., C. T. ATKINSON, AND R. E. CARLETON. 1994. *Sarcocystis* sp. in wading birds (Ciconiiformes) from Florida. *Journal of Wildlife Diseases* 30: 29–35.
- STALLKNECHT, D. E., AND S. M. SHANE. 1988. Host range of avian influenza virus in free-living birds. *Veterinary Research Communications* 12: 125–141.
- STAMM, D. D., AND R. J. NEWMAN. 1963. Evidence of southward transport of arboviruses from the U.S. by migratory birds. *Annals of Microbiology* 11: 123–133.
- SUAREZ, D. L. 2000. Evolution of avian influenza viruses. *Veterinary Microbiology* 74: 15–27.
- SYRŮČEK, L., AND K. RAŠKA. 1956. Q fever in domestic and wild birds. *Bulletin of the World Health Organisation* 15: 329–337.
- TER-VARTANOV, V. N., V. M. GUSEV, P. A. REZNIK, A. A. GUSEVA, M. N. MIRZOEVA, O. N. BOCHARNIKOV, AND N. N. BAKEEV. 1956. Transport of ticks and fleas by birds. *Zoologicheskii Zhurnal* 35: 173–189. [In Russian.]
- THEILER, M., AND W. G. DOWNS. 1973. The arthropod-borne viruses of vertebrates. Yale University Press, New Haven, Connecticut–London, UK, 578 pp.
- UPTON, S. J., AND R. D. MCKOWN. 1992. The red-tailed hawk, *Buteo jamaicensis*, a native definitive host of *Frenkelia microti* (Apicomplexa) in North America. *Journal of Wildlife Diseases* 28: 85–90.
- URYVAEV, L. V., V. A. VASILENKO, N. A. PARASYUK, K. S. JONOVA, E. A. GUSHCHINA, A. A. KULLAPERRE, E. LEJBAL, AND D. K. LVOV. 1992. Isolation and identification of Sindbis virus from migratory birds in Estonia. *Voprosy Virusologii* 37: 67–70. [In Russian.]
- VALKIUNAS, G. A. 1989. Peculiarities of the distribution of birds infected with haemosporidians (Sporozoa, Haemosporidia) during their autumn migration along flight waves. *Parazitologia* 23: 377–382. [In Russian.]
- . 1991. On the pathogenic influence of haemoproteids (Haemosporidia: Haemoproteidae) on wild birds in field conditions. *Parazitologia* 25: 404–411. [In Russian.]
- VAN UDEN, N., AND R. C. CASTELO-BRANCO. 1963. Distribution and population densities of yeast species in Pacific water, air, animals, and keep off Southern California. *Limnology and Oceanography* 8: 323–329.
- VARMA, M. G. R., E. T. W. BOWEN, D. I. H. SIMPSON, AND J. CASALS. 1973. Zirqa virus, a new arbovirus isolated from bird-infesting ticks. *Nature* 244: 452.
- WALLACE, J. S., T. CHEASTY, AND K. JONES. 1997. Isolation of Vero cytotoxin-producing *Escherichia coli* O157:H7 from wild birds. *Journal of Applied Microbiology* 82: 399–404.
- WALTER, C., A. LIEBISCH, AND C. VAUK. 1979. Untersuchungen zur Biologie und Verbreitung von Zecken (Ixodoidea, Ixodidae) in Norddeutschland, II. Zecken der Zugvögel auf der Insel Helgoland. *Zeitschrift für die angewandte Zoologie* 66: 445–461.
- WARNER, C. M., AND D. W. FRENCH. 1970. Dissemination of fungi by migratory birds: Survival and recovery of fungi from birds. *Canadian Journal of Botany* 48: 907–910.
- WATSON, G. E., R. E. SHOPE, AND M. N. KAISER. 1972. An ectoparasite and virus survey of migratory birds in the eastern Mediterranean. *In* Transcontinental connections of migratory birds and their role in the distribution of arboviruses,

- A. I. Cherepanov (ed.). Nauka, Novosibirsk, Russia, pp. 176–180.
- WEBSTER, R. G., W. J. BEAN, O. T. GORMAN, T. M. CHAMBERS, AND Y. KAWAOKA. 1992. Evolution and ecology of influenza A viruses. *Microbiological Reviews* 56: 152–179.
- WEISBROD, A. R., AND R. C. JOHNSON. 1989. Lyme disease and migrating birds in the Saint Croix river valley. *Applied and Environmental Microbiology* 55: 1921–1924.
- WEISSENBOCK, H., J. KOLODZIEJEK, A. URL, H. LUSZY, B. REBEL-BAUDER, AND N. NOWOTNY. 2002. Emergence of Usutu virus, an African mosquito-borne *Flavivirus* of the Japanese encephalitis virus group, Central Europe. *Emerging Infectious Diseases* 8: 652–656.
- WEST, P. A., J. V. LEE, AND T. N. BRYANT. 1983. A numerical taxonomic study of species of *Vibrio* isolated from the aquatic environment and birds in Kent, England, U.K. *Journal of Applied Bacteriology* 55: 263–282.
- WOBESER, G. A. 1997. Diseases of wild waterfowl, 2nd Edition. Plenum Press, New York, New York, 324 pp.
- WOOD, A. J., AND T. J. TRUST. 1972. Some qualitative and quantitative aspects of the intestinal microflora of the glaucous-winged gull (*Larus glaucescens*). *Canadian Journal of Microbiology* 18: 1577–1583.
- WORK, T. H. 1958. Russian spring-summer virus in India: Kyasanur Forest disease. *Progress in Medical Virology* 1: 248–279.
- , AND R. D. LORD. 1972. Trans-Gulf migrants and the epizootiology of arboviruses in North America. In *Transcontinental connections of migratory birds and their role in the distribution of arboviruses*, A. I. Cherepanov (ed.). Nauka, Novosibirsk, Russia, pp. 207–214.
- YUNKER, C. E. 1975. Tick-borne viruses associated with seabirds in North America and related islands. *Medical Biology* 53: 302–311.

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