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AVIAN INFLUENZA IN MIGRATORY BIRDS IN THE UNITED STATES, 2007–2009, AND EFFECTS OF SEPTEMBER HUNTING SEASONS ON SURVIVAL, HARVEST, AND RECOVERY RATES OF CANADA GEESE BANDED IN SOUTHEAST NEBRASKA

by

Scott Ryan Groepper

A THESIS

Presented to the Faculty of

The Graduate College at the University of Nebraska

In Partial Fulfillment of Requirements

For the Degree of Master of Science

Major: Natural Resource Sciences

Under the Supervision of Professor Scott E. Hygnstrom

Lincoln, Nebraska

August, 2011

AVIAN INFLUENZA IN MIGRATORY BIRDS IN THE UNITED STATES, 2007–2009, AND EFFECTS OF SEPTEMBER HUNTING SEASONS ON SURVIVAL, HARVEST, AND RECOVERY RATES OF CANADA GEESE BANDED IN SOUTHEAST NEBRASKA

Scott Ryan Groepper, M.S.

University of Nebraska, 2011

Adviser: Scott E. Hygnstrom

Highly-pathogenic avian influenza virus (HPAIV H5N1) poses risks to wild birds, poultry, and humans. Personnel with the United States Department of Agriculture-Animal Plant Health Inspection Service-Wildlife Services, state, and tribal wildlife agencies collected 168,940 samples from migratory birds from 2007 to 2009 to test for presence of HPAIV H5N1. No HPAIV was found, but other subtypes were discovered, including H5 and H7. I estimated prevalence of avian influenza virus by flyway and found prevalence was lowest each year in the Atlantic Flyway (6.7%–8.3%), highest in the Pacific Flyway in 2007 (13.3%) and 2008 (13.4%), and highest in the Mississippi Flyway in 2009 (15.9%). I plotted prevalence monthly and found August–November was optimal time for sampling due to highest prevalence in all flyways. Dabbling ducks had significantly higher prevalence of AIV ($\overline{x} = 14.1\%$, range = 9.3%–19.4%) than other functional groups across all flyways and study years. My results suggest future surveillance should focus on species from the dabbling duck functional group.

Restoration efforts in Nebraska have contributed to increased populations of resident Canada geese (*Branta canadensis*) that now are considered a nuisance. In 2004, an early September hunting season was initiated to reduce populations. I analyzed band

returns from geese banded in Nebraska to determine if early September hunting seasons affected survival, harvest, and recovery rates. The top model in my survival analysis revealed early September hunting seasons did not reduce survival (S = 0.696) of geese. In addition, models indicated survival was not different between geese inside and outside the early hunting zone (southeast vs. northeast, S = 0.711) and survival did not differ by sex (S = 0.708). Survival differed between the metropolitan areas of Omaha and Lincoln, Nebraska (S = 0.742 and 0.678, respectively). A combination of urbanization and nonmigratory behavior may be leading to higher survival of Canada geese in Nebraska.

DEDICATION

I dedicate this work to my wife Carrie and my 3 sons, Colby, Camden, and Quenten. Without your love and support, my accomplishments, academic, professional, and personal would be meaningless.

ACKNOWLEDGEMENTS

I would like to thank Dr. Mark Vrtiska. Mark took a chance on me and gave me the opportunity to succeed. The knowledge of waterfowl management and ecology he has shared with me over the past 4 years is priceless. Mark has been a trusted friend and I hope that continues well into the future. I would like to thank my adviser Dr. Scott Hygnstrom. He was the force that pulled this research project together, forging a cooperative agreement between the University of Nebraska, Nebraska Game and Parks, and the United States Department of Agriculture-Wildlife Services. In addition, I thank the members of my graduate committee, Dr. Larkin Powell, and Dr. Thomas DeLiberto for their valuable input on study design and data analysis and allowing me access to data. Todd Buckley assisted me with modeling and was a good friend and confidant. Adam Schole served as my full-time technician in 2010 and helped with collection starting in 2007. I've never met anyone with a more positive outlook and outstanding work ethic; it was my pleasure to work with him and he is a good friend. I thank my parents, Ron and Colleen; they've supported me through all the highs and lows and have always been a positive force in me and my family's lives.

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CHAPTER 1: EXCUTIVE SUMMARY AVIAN INFLUENZA IN MIGRATORY BIRDS IN THE UNITED STATES, 2007–2009

Scott Ryan Groepper, M.S.

University of Nebraska-Lincoln, 2011

Adviser: Professor Scott E. Hygnstrom

Highly-pathogenic avian influenza virus (HPAIV H5N1) poses risks to wild birds, poultry, and humans. Personnel with the United States Department of Agriculture-Animal Plant Health Inspection Service-Wildlife Services, state, and tribal wildlife agencies collected 168,940 samples from migratory birds throughout the United States from 2007 through 2009 to test for presence of HPAIV H5N1. Migratory birds from the following functional groups were collected: dabbling duck, diving duck, goose and swan, shorebird, gull and tern, and other water birds. No HPAIV was found, but combinations of the 16 hemagglutinin (H) and 9 neuraminidase (N) AIV subtypes were discovered, including H5 and H7 subtypes. I estimated prevalence of AIV by North American flyway and found prevalence was lowest each year in the Atlantic Flyway (range = 6.7% - 8.3%), highest in the Pacific Flyway in 2007 (13.3%) and 2008 (13.4%), and highest in the Mississippi Flyway in 2009 (15.9%). I plotted prevalence of AIV monthly and found August– November was the optimal period for sampling in all flyways so future surveillance efforts should be concentrated during this period. I found that dabbling ducks had significantly higher prevalence of AIV ($\overline{x} = 14.1\%$, range = 9.3%–19.4%; P < 0.001) than other functional groups across all flyways and study years. American green-winged

teal (*Anas creeca*, range = 9%–22%), blue-winged teal (*A. discors*, range = 8%–22%), mallards (*A. platyrhynchos*, range = 12%–27%), northern pintails (*A. acuta*, range = 3%– 28%), and northern shovelers (*A. clypeata*, range = 4%–21%) were species with high prevalence and most often sampled by participating agencies. My results suggest future surveillance for AIV should focus on species from the dabbling duck functional group.

EFFECTS OF SEPTEMBER HUNTING SEASONS ON SURVIVAL, HARVEST, AND RECOVERY RATES OF CANADA GEESE BANDED IN SOUTHEAST NEBRASKA

Scott Ryan Groepper, M.S.

University of Nebraska-Lincoln, 2011

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Restoration efforts in Nebraska have contributed to increased populations of resident Canada geese (*Branta canadensis*). Populations have grown to levels that now are considered a nuisance and damage has exceeded public tolerance. An early September hunting season was initiated in southeast Nebraska in 2004 to reduce populations of resident Canada geese. We analyzed band returns from geese banded in southeast Nebraska from 1999 to 2010, to determine if early seasons affected survival, harvest, and recovery rates. Our survival analysis revealed that early hunting seasons did not reduce survival of geese (S = 0.696, 95% C.I. = 0.679-0.713, S' = 0.896, 95% C.I. = 0.786-0.953). In addition, survival was not different between geese inside and outside the early hunting zone (southeast versus northeast Nebraska, S = 0.711, 95% C.I. = 0.666-

0.752) and survival did not differ by sex, but varied yearly (S = 0.630-0.816). We detected differences in survival between the metropolitan areas of Omaha (S = 0.742, 95% C.I. = 0.688-0.790) and Lincoln, Nebraska, (0.678, 95% C.I. = 0.651-0.703). Seventy-three percent of all recoveries of geese banded after hatch-year and 71% of all recoveries of geese banded hatch-year were from Nebraska. The September hunting season affected timing of recovery as 23%-49% of annual band recoveries for the hunting season occurred during the month of September. Prior to initiation of September hunting seasons, November was the month with the highest number of recoveries of both AHY and HY geese (27% and 38%, respectively). A high degree of urbanization in this region of the state may be leading to higher survival and control methods other than hunting should be explored to reduce populations.

CHAPTER 2: LITERATURE REVIEW

AVIAN INFLUENZA

Highly-pathogenic avian influenza virus (HPAIV) H5N1 emerged in China in 1996–1997 (Subbarao et al., 1998) and has since spread to other areas of Asia, the Middle East, Europe and Africa despite control efforts (Pfeiffer, 2007). Highly-pathogenic AIV H5N1 can result in significant morbidity in poultry, waterfowl, and humans. Thousands of migratory waterfowl succumbed to HPAIV H5N1 in the initial wild bird outbreak at Qinghai Lake, China (Chen et al., 2005) and subsequent outbreaks worldwide. Millions of domestic poultry have been culled to slow the spread of HPAIV (Iwami et al., 2009). The HPAIV H5N1 can be transmitted directly from birds to humans (Claas et al., 1998; Guan et al., 2004; Peiris et al., 2004) with 552 human cases and 324 deaths reported ([58%]; World Health Organization, 2011).

Wild waterfowl are a reservoir and an important long-term evolutionary source for influenza A viruses (Sturm-Ramirez et al., 2005). Influenza A viruses of 16 hemagglutinin (H) and 9 neuraminidase (N) combinations typically are non-pathogenic and cause natural infections in wild birds; only the H5 and H7 subtypes have caused HPAIV in avian species (Alexander, 2000; Olsen et al., 2006). Influenza viruses have been isolated in 13 orders of birds, but mostly in *Anseriformes* and *Charadriiformes* (Stallknecht and Shane, 1988; Gilbert et al., 2006). Species in these orders are thought to be particularly susceptible because they are exposed to shallow water that may be contaminated with infected fecal or oral material, especially during fall congregations (Sturm-Ramirez et al., 2005; Rappole and Hubalek, 2006). Species from the family *Anatidae* pose the highest risk for transmission to other waterfowl and domestic poultry because they may excrete large amounts of virus and remain healthy while moving large distances (Delogu et al., 2003; Hulse-Post et al., 2005; Gaidet et al., 2010). Concern has been raised about the role wild birds play in harboring, perpetuating, and transmitting AIV to new geographic locations, internationally and intercontinentally (Guberti and Newman, 2007; Boyce et al., 2009). Highly-pathogenic AIVs evolve in domestic poultry from low-pathogenic avian influenza viruses (LPAIV) that circulate widely in birds (Webster et al., 1992; Alexander et al., 1993). Different influenza subtypes also can infect ducks concomitantly, creating the opportunity for genetic mixing (Sharp et al., 1997). Low-pathogenic AIVs cause mild respiratory diseases that may be exacerbated by other infections or extreme environmental conditions (Alexander, 2000). Clinical signs of HPAIV H5N1 infection in waterfowl include paralysis, unusual head tilt, staggering, and death (Chen et al., 2005).

Outbreaks of HPAIV H5N1 in the past have involved dead or dying birds during periods of environmental or physiological stress, suggesting the virus is highly lethal and ability of birds to carry the virus long distances would be impaired (Feare and Yasue, 2006; Feare, 2010). Conversely, Gaidet et al. (2010) reported that waterfowl may be able to spread HPAIV H5N1 long distances (> 350 km) during migration periods due to differing asymptomatic infection duration periods in different species. Two studies demonstrated apparently healthy waterfowl positive for HPAIV H5N1 in China and Russia (Chen et al., 2006*b*; Lvov et al., 2006) but questions concerning methodology, sampling, and identification of these waterfowl have been raised (Feare and Yasue, 2006). In 2010, HPAIV H5N1 was isolated from a healthy mallard (*Anas platyrhynchos*) in South Korea (Kim et al., 2011 *in press*). In addition, a hunter harvested a mallard in

2009 and a mute swan (*Cygnus olor*) in 2007, in Germany, both had no clinical signs of HPAIV H5N1, but upon testing were found positive (World Organization for Animal Health, 2009; Breed et al., 2010). Some species of waterfowl, especially mallards, can potentially be long-distance vectors of HPAIV H5N1 (Keawcharoen et al., 2008). In 2008, samples from a clinically healthy common pochard (*Aythya farina*) were collected in Switzerland as part of HPAIV H5N1 surveillance (Baumer et al., 2010). The results of the real-time reverse transcriptase polymerase chain reaction (rRT-PCR) assay were positive for H5N1 indicating the species may be a vector for H5N1. In Nigeria, HPAIV H5N2 was detected in a healthy white-faced whistling duck (*Dendrocygna viduata*) and a spur-winged goose ([*Plectroplerus gambensis*]; Gaidet et al., 2008). Genetic similarities between HPAIV H5N1 isolated from migratory waterfowl at 2 locations separated by 1,700 km in China suggest that the virus can be carried long distances (Chen et al., 2006*a*)

Kalthoff et al. (2008) experimentally infected mute swans (*Cygnus olor*) with HPAIV H5N1 and found birds inoculated with low doses of virus died 3–5 days later than birds inoculated with high doses of virus (8–14 days) and 1 bird in the low dosage group survived. In addition, the authors inoculated 2 birds with high doses of H5N1 that had previous exposure to AIV and both survived. One of 4 cackling geese (*Branta hutchinsii*) and 3 of 5 bar-headed geese (*Anser indicus*) survived experimental inoculation with HPAIV H5N1 (Brown et al., 2008). Brown et al. (2006), inoculated blue-winged teal (*Anas discors*), mallards, northern pintails (*A. acuta*), and redheads (*A. americana*) with Asian HPAIV H5N1 strains and observed no mortality in these species. Conversely, the authors found wood ducks (*Aix sponsa*) and laughing gulls (*Larus* *atricilla*) were more susceptible to HPAIV H5N1 with reported mortality between 50% and 66%. Keawcharoen et al. (2008) inoculated tufted ducks (*A. fuligula*), Eurasian pochards (*A. ferina*), mallards, common teal (*A. crecca*), Eurasian wigeon (*A. penelope*), and gadwall (*A. strepera*) with HPAIV H5N1 and only observed mortality in tufted ducks and Eurasian pochards: ducks from the genus *Anas* were clinically unaffected. Highly-pathogenic H5N1 has been isolated in 152 species of wild birds (US Geological Survey, 2010) since an outbreak of HPAIV H5N3 in common terns (*Sterna hirundo*) in South Africa in 1961 (Becker, 1966).

Migration of waterfowl in North America generally follows 4 major flyways: the Atlantic, Mississippi, Central, and Pacific (Lincoln, 1935; Figure 2-1). Alaska and the Pacific Flyway are thought to be the most likely points of introduction of wild waterfowl infected with HPAIV to North America because of proximity to Siberia and the East Asia Flyway (DeLiberto et al., 2009). Three pathways are used annually by waterfowl between hemispheres: Alaska–East Asia, East Asia–Pacific North America and Europe–Atlantic North America (Rappole and Hubalek, 2006). Given that migratory birds pose a risk of HPAIV entry into the US, surveillance in areas where intercontinental migrants enter the country, such as Alaska, may yield the first evidence of introduction (US Department of Agriculture, [USDA] 2006; DeLiberto et al., 2009). Thirty-three species of waterfowl, 46 species of shorebirds, and 15 species of gulls and terns equaling an estimated 1.5–2.9 million individuals move from Asia to North America and vice versa each year (Winker and Gibson, 2010). Satellite telemetry data from migrating northern pintails revealed crossover between Alaska and Russia (Miller et al., 2005). Genetic analyses of AIVs suggest that exchange of viruses between Eurasian and American clades does not occur

frequently and introduction of HPAIV to North America by migratory birds would be unlikely via the Alaska-East Asia pathway (Webster et al., 1992; Olsen et al., 2006; Krauss et al., 2007). Conversely, a study of LPAIV in northern pintails in Alaska found 45% of viruses had gene segments more closely related to Asian strains than North American strains (Koehler et al., 2008). Wahlgren et al. (2008) described isolation of H6N1 from a Dunlin (*Calidris alpina*) collected in Alaska that had gene segments more closely related to Asian lineages of AIV than North American lineages of AIV. Surveillance of domestic ducks in South Korea discovered H3N2 AIV that was more closely related to the North American strain than the Eurasian strain (Kang et al., 2009). In India, H11N1 was isolated from surveillance of live wild birds (Pawar et al., 2010). The authors found that the virus was related to AIV isolated in shorebirds in Delaware, US, in 2000 and 2003. An American wigeon (A. americana) collected in Sonora, Mexico was infected with H9 AIV that was more closely related to Eurasian H9 isolates than North American isolates (Montalvo-Corral and Hernandez, 2010). The H5 subtype is uncommon in migratory birds in North America and was detected in only 555 of 145,055 samples collected from 2006–08 ([0.4%]; DeLiberto et al., 2009; Pedersen et al., 2010). Ninety-one percent of H5 detections in North America were from dabbling ducks and 48% were found in mallards (Pedersen et al., 2010).

The risk of introduction of HPAIV into the United States by a single pathway is relatively low (Kilpatrick et al., 2006). Human and commercial activities, particularly those associated with the poultry industry are major factors that have influenced global dispersal (Gauthier-Clerc et al., 2007; Brown, 2010; Li et al., 2011). Some authors have argued that waterfowl infected with HPAIV would be too morbid or die before they would be able to spread virus long distances (Perkins and Swayne, 2003; Olsen et al., 2006), but 3 major events during 2005–2006 refute those arguments. In 2005, a major outbreak of HPAIV H5N1 occurred in bar-headed geese at Qinghai Lake, China. This outbreak was followed by detection of the virus in Mongolia, Russia, Turkey, Romania, and Ukraine near wintering sites of migratory waterfowl. Mute swans and other waterfowl infected with HPAIV H5N1 were detected in Western Europe in the spring of 2006, independent of a concurrent poultry outbreak (Chen et al., 2005; Liu et al., 2005; Chen et al., 2006*b*; Gilbert et al., 2006). Migratory birds have been implicated in the spread of HPAIV into Japan where importation of poultry from HPAIV-endemic areas was banned (Mase et al., 2005; Uchida et al, 2008) and first detection of HPAIV H5N1 in Africa occurred when viruses showing common phylogeny were present in Eurasian wild migratory birds suggesting genetic relationships to central Russian AIVs (Salzberg et al., 2007; Starick et al., 2008; Cattoli et al., 2009).

Waterfowl commonly congregate in permanent wetlands with dense emergent vegetation after breeding where juveniles mature, adults molt, and species mix before migration, which leads to increased risk of spreading AIV (Gilbert et al., 2006). Congregations of waterfowl may lead to high prevalence of AI in naïve juveniles just before fall migrations (Fouchier et al., 2007; Webster et al., 2007; Munster and Fouchier, 2009). Prevelance of AIV declines on wintering grounds as immunity of flocks build (Halvorson et al., 1985; Munster et al., 2007; Wallensten et al., 2007). Pink-footed geese (*A. brachyrhynchus*) had higher prevalence of AIV (63%) in November–January on their over-wintering location than at any other time or location ([0%]; Hoye et al., 2011) and reported prevalence of AIV was as high as 9.5% in mallards in March–June (Wallensten

et al., 2007). Eighty-eight percent of positive samples for AIV in Iran were collected in February and March (Ferdidouni et al., 2010).

The best opportunities for viral transmission among large numbers of Anseriformes hosts may be on lakes and ponds in summer where large concentrations of birds gather for weeks to undergo the post-breeding, pre-migratory molt (Webster et al., 1992). Survival of AIVs outside hosts is affected by humidity, ultraviolet radiation, water salinity, and temperature (Brown et al., 2007; Weber and Stilianakis, 2008; Shahid et al., 2009; Zuk et al., 2009). Estimated survival duration of HPAIV H5N1 acquired from poultry in Korea was 930-3,213 days in 4°C water (Paek et al., 2010). Persistence of HPAIV H5N1 was longer (> 60 days) at 4°C water than in 20°C water ([14–21 days]; Domanska-Blicharz et al., 2010). Survival of HPAIV H5N1 was 350 days in -10°C water while survival was only 13 days in 30°C water (Nazir et al., 2010). Eight H5 and H7 LPAIVs persisted for 128-375 days and 2 HPAIV H5N1 persisted for 82-182 days in 17°C water while those same LPAIVs and HPAIVs persisted for 19–61 days and 28 days in 28°C water, respectively (Brown et al., 2007). Survival of AIVs in water suggests the possibility of an environmental reservoir, but rapid loss of infectivity has been observed in freeze-thaw experiments (Stallknecht et al., 2010). Outbreaks in wild birds may be associated with periods of environmental or physiological stress (Globig et al., 2009). Avian influenza infection in migratory birds can vary greatly according to season and location because species exhibit different migratory behaviors, habitat preferences, and geographic ranges (Stallknecht and Brown, 2007). Timing relative to migration is the determinant of prevalence of influenza A virus (Munster and Fouchier, 2009).

Important migratory stop-over areas such as the Rainwater Basin of Nebraska hold potential for concentrating waterfowl and shorebirds, which could lead to virus transmission. In the spring of 2001, an estimated 7.2 million lesser snow geese (*Chen caerulescens*) and Ross's geese (*C. rossii*) were observed in the Rainwater Basin and Platte River Valley of Nebraska (Vrtiska and Sullivan, 2009). The Delaware Bay located between Delaware and New Jersey, in the Atlantic Flyway, concentrates nearly the entire population of red knots (*Calidris canutus*) during migration (Myers, 1986) and other species of shorebirds and waterfowl often exceeding 1 million individuals (Hanson et al., 2008). The Copper River Delta of Alaska, in the Pacific Flyway, has the largest spring concentrations of migratory shorebirds with up to 5 million birds per day (Bishop et al., 2000).

We reviewed recent literature comparing oropharyngeal and cloacal samples for detection of AIV. More HPAIV H5N1is excreted via the respiratory tract than the intestinal tract (Sturm-Ramirez et al., 2005; Suarez et al., 2007; Keawcharoen, et al. 2008). Considerably larger numbers (62%) of oropharyngeal versus cloacal (29%) samples were positive for LPAIV collected from the same dabbling ducks in Minnesota (Jindal et al., 2010). Similar results were found by Parmley et al. (2011) when comparing virus detection (33% and 26% for oropharyngeal versus cloacal swabs, respectively). Oropharyngeal samples collected from greater white-fronted geese (*Anser albifrons*) in Europe had 2.4 times higher detection frequency than cloacal samples (Kleijn et al., 2010). In addition, Bulaga et al. (2003) found tracheal samples yielded AIV more often than cloacal or environmental samples. Ferdidouni et al. (2010) found a similar proportion of positive oropharyngeal and cloacal samples from waterbirds in Iran, but they conceded the number of LPAIV positive birds may be underestimated when only collecting cloacal swabs.

RESIDENT CANADA GEESE

Restoration of Canada geese (*Branta canadensis*) is considered a success story of 20th century wildlife management and populations in the US have increased an average of 6.2% per year since the mid-1970s (Schmidt, 2004). Canada geese have become common inhabitants of urban areas due to abundant and stable nesting habitat, plentiful food sources, few predators, and habituation to humans (Groepper et al., 2008). Canada geese provide recreational opportunities and most residents approve of the presence of Canada geese in their communities but complaints may increase as damage and nuisance problems become more widespread as populations increase (Coluccy et al., 2001; Powell et al., 2004).

Populations of Canada geese have exceeded management objectives in the Atlantic, Mississippi, and Central Flyways and the increasing populations have resulted in nuisance problems (Gabig, 2000). Goose-related problems, including depredation of agricultural crops, airport hazards, fecal contamination of water, and damage to lawns, parks, beaches, and golf courses have increased (Gosser et al., 1997; Coluccy et al., 2004). Control of population growth of temperate nesting Canada geese where they have exceeded public tolerance levels will be a continuing focus of managers in the future (Moser and Caswell, 2004).

Hunting is the primary cause of mortality in Canada geese (Krohn and Bizeau, 1980) and early September hunting seasons have been implemented to reduce populations of resident Canada geese while causing little or no impact to migratory geese (Gabig 2000; Coluccy et al., 2004; Vrtiska et al., 2004; Sheaffer et al., 2005). South Dakota was the first state in the Central Flyway to initiate a September season in 1996, followed by North Dakota and Kansas (1999), Oklahoma (2000), and Nebraska ([2004]; Vrtiska et al., 2004). Relatively few studies have been conducted to determine effects of special hunting seasons on resident Canada geese (Heusmann, 1999; Sheaffer et al., 2005; Dieter et al., 2010) and survival and harvest parameters are important for management decisions (Gabig, 2000; Vrtiska et al., 2004).

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Figure 2-1. The major migratory bird flyways of the US (Lincoln, 1935).

CHAPTER 3: AVIAN INFLUENZA VIRUS PREVALENCE AND TIMING BY

FLYWAY, UNITED STATES, 2007–2009.

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Abstract: Highly-pathogenic avian influenza virus (HPAIV H5N1) poses risks to wild birds, poultry, and humans. The US Department of Agriculture-Animal Plant Health Inspection Service-Wildlife Services (USDA-APHIS-WS), state, and tribal wildlife agencies collected 168,940 samples from migratory birds in the US from 2007 to 2009 as part of an interagency early detection system for HPAI. No HPAIV was detected, but combinations of the 16 hemagglutinin (H) and 9 neuraminidase (N) subtypes of low-pathogenic avian influenza viruses (LPAIV) were discovered, including H5 and H7 subtypes. We estimated apparent prevalence of AIV by North American flyway and found it was lowest each year in the Atlantic Flyway (range = 6.7%–8.3%), highest in the Pacific Flyway in 2007 (13.3%) and 2008 (13.4%), and highest in the Mississippi Flyway in 2009 (15.9%). We also plotted apparent prevalence of AIV monthly and determined fall peaks in AIV infection occurred in September in the Atlantic Flyway, and August and

December in the Pacific Flyway. We suggest that annual sampling for AIV coincide with these peaks in prevalence by flyway.

Key words: avian influenza, flyway, functional group, highly-pathogenic, low-pathogenic, prevalence, timing, waterfowl

Abbreviations: AIC = Akaike's Information Criterion, AIV = avian influenza virus, , AUC = area under the receiver operating curve, BIC = Bayesian Information Criterion, FG = functional group, FW = flyway, GLMM = generalized linear mixed model, H = hemagglutinin, HPAIV = highly-pathogenic avian influenza virus, Lat = latitude, LPAIV = low-pathogenic avian influenza virus, N = neuraminidase, PN = positive/negative avian influenza infection, PROC FREQ = frequency procedure, PROC REG = regression procedure, ROC = receiver operating curve, rRT-PCR = real-time reverse transcriptase polymerase chain reaction, SAS = Statistical Analysis Software, USDA-APHIS-WS = US Department of Agriculture- Animal Plant Health Inspection Service-Wildlife Services

INTRODUCTION

Wild waterfowl are reservoirs and an important long-term evolutionary source for all influenza A viruses, which usually are non-pathogenic (Sturm-Ramirez et al., 2005; Olsen et al., 2006). Highly-pathogenic AIVs are thought to evolve in domestic poultry from low-pathogenic avian influenza viruses (LPAIV) that circulate widely in birds (Webster et al., 1992; Alexander et al., 1993). Different influenza subtypes can infect ducks concomitantly, creating the opportunity for genetic mixing (Sharp et al., 1997). Low-pathogenic AIVs cause mild respiratory diseases that may be exacerbated by other infections or extreme environmental conditions (Alexander, 2000). Influenza A viruses have been isolated in 13 orders of birds but most have been observed in *Anseriformes* and *Charadriiformes* (Stallknecht and Shane, 1988; Gilbert et al., 2006). Species in these orders are thought to be particularly susceptible, especially during fall congregations, because they are exposed to shallow water that may be contaminated with infected fecal or oral matter (Sturm-Ramirez et al., 2005; Rappole and Hubalek, 2006). Highlypathogenic AIV H5N1 has been reported in 152 species of wild birds worldwide (US Geological Survey, 2010) since an outbreak of HPAIV H5N3 in common terns (*Sterna hirundo*) in South Africa in 1961 (Becker, 1966).

Species from the family *Anatidae* pose the highest risk for transmission to other waterfowl and domestic poultry because they can excrete large amounts of virus and can remain healthy while moving large distances (Delogu et al., 2003; Hulse-Post et al., 2005; Gaidet et al., 2010). Concern has been raised about the role of wild birds in harboring, perpetuating, and transmitting AIV to new geographic locations both internationally and intercontinentally (Guberti and Newman, 2007; Boyce et al., 2009). Migratory animals are considered to be at a higher risk of infection from more diverse parasite fauna, highlighting the potential importance of populations in the ecology and epidemiology of diseases (Figuerola and Green, 2000).

Migration of waterfowl in North America generally follows 4 major flyways: the Atlantic, Mississippi, Central, and Pacific (Lincoln, 1935; Figure 3-1). The Pacific Flyway and Alaska are thought to be the most likely points of introduction of wild waterfowl infected with HPAIV to North America because of proximity to Siberia and the East Asia Flyway (DeLiberto et al., 2009). Three migratory pathways are used annually by waterfowl between hemispheres: Alaska–East Asia, East Asia–Pacific North America, and Europe–Atlantic North America (Rappole and Hubalek, 2006). Given that migratory birds pose a risk of HPAIV entry into the US, surveillance in areas where intercontinental migrants enter the country, such as Alaska, may yield the first evidence of introduction (US Department of Agriculture [USDA], 2006; DeLiberto et al., 2009).

Thirty-three species of waterfowl, 46 species of shorebirds, and 15 species of gulls and terns estimated at 1.5–2.9 million individuals move between Asia to North America and vice versa yearly (Winker and Gibson, 2010). Genetic analysis of AIVs suggested that exchange between Eurasian and American clades does not occur frequently and introduction of HPAIV to North America by migratory birds would be unlikely (Webster et al., 1992; Olsen et al., 2006; Krauss et al., 2007). Conversely, a study of LPAIV in northern pintails (*A. acuta*) in Alaska found 45% of viruses had gene segments more closely related to Asian strains than North American strains (Koehler et al., 2008). Other studies have reported isolation of AIVs that show evidence of intercontinental exchange (Wahlgren et al., 2008; Kang et al., 2009; Montalvo-Corral and Hernandez, 2010; Pawar et al., 2010). The H5 subtype is uncommon in birds in North America and was detected in 555 of 145,055 samples (0.4%) collected from 2006 to 2008 (DeLiberto et al., 2009; Pedersen et al., 2010). Dabbling ducks accounted for 91% of H5 detections in North America (Pedersen et al., 2010).

After nesting, waterfowl commonly congregate on permanent wetlands with dense emergent vegetation where juveniles mature, adults molt, and species mix before migration, which can lead to increased risk of spreading AIV (Webster et al., 1992; Gilbert et al., 2006). Congregations of waterfowl may lead to high prevalence of AIV in naïve juveniles before fall migrations (Fouchier et al., 2007; Webster et al., 2007; Munster and Fouchier, 2009). Prevalence of AIV declines on wintering grounds as immunity builds in flocks (Halvorson et al., 1985; Munster et al, 2007; Wallenstern et al., 2007). Other studies have reported higher prevalence of AIV during the over-winter and spring periods (Fereidouni et al., 2010; Hoye et al., 2011). Outbreaks in wild birds have been associated with periods of environmental or physiological stress (Globig et al., 2009). Prevalence of AIV among migratory birds can vary by season and location, because species exhibit different migratory behaviors, habitat preferences, and geographic ranges (Stallknecht and Brown, 2007).

Important migratory stop-over areas such as the Rainwater Basin of Nebraska in the Central Flyway hold the potential for concentrating waterfowl, leading to virus transmission. In the spring of 2001, an estimated 7.2 million snow geese (*Chen caerulescens*) and Ross's geese (*C. rossii*) were observed in the Rainwater Basin and Platte River Valley of Nebraska (Vrtiska and Sullivan, 2009). In addition, the Delaware Bay, in the Atlantic Flyway, concentrates nearly the entire population of red knots (*Calidris canutus*) during migration (Myers, 1986) and other species of shorebirds, gulls, and waterfowl often exceeding 1 million individuals (Hanson et al., 2008). In the Pacific Flyway, the Copper River Delta in Alaska holds the largest spring concentration of migratory shorebirds in the Western Hemisphere, with up to 5 million birds per day (Bishop et al., 2000).

It is important for structuring future surveillance efforts that we understand how prevalence of AIV is distributed spatially and temporally and how it spreads through populations. The objectives of this study were to determine apparent prevelance of AIV by: 1) flyway, 2) year, and 3) month. We predicted the highest apparent prevalence of AIV would occur in July–September due to influx of congregations of immonulogically naive hatch-year birds. Our results provide a comprehensive overview of apparent prevalence of AIV by US flyway and peaks in apparent prevalence of AIV.

MATERIALS AND METHODS

Personnel with the USDA-Animal Plant Health Inspection Service-Wildlife Services (APHIS-WS) and state and tribal wildlife agencies collected 168,940 samples from migratory birds in the US for early detection of HPAIV during 2007–2009, using standardized protocols and procedures (USDA, 2006; DeLiberto et al., 2009; Pedersen et al., 2010). The USDA identified 5 collection strategies in the US Strategic Plan: live wild bird, sentinel, hunter harvest, and morbidity/mortality investigation, and environmental sampling (USDA, 2006; DeLiberto et al., 2009). We conducted sampling by biological year (April 1–March 31) from 2007 to 2009. Personnel collected cloacal and oropharyngeal samples from birds using sterile dacron-tipped swabs (Puritan, Puritan Medical Products LLC) and combined them in vials containing 3 mL of brain-heart infusion broth (Becton Dickinson, Franklin Lakes, NJ). Samples were kept cool, not frozen, and shipped to National Animal Health Laboratory Network laboratories within 72 hours of collection (usually within 24 hours). Samples were screened for type A influenza with matrix real-time reverse transcriptase polymerase chain reaction (rRT-PCR) assay (Spackman et al., 2002) within 48 hours of receipt of samples. If a sample screened positive for H5 or H7, it was shipped to the National Veterinary Services Laboratory in Ames, IA for isolation, sub-typing, and pathogenicity testing. The US Strategic Plan (USDA, 2006) identified lists of migratory birds with potential exposure to HPAIV H5N1. The primary focus of sampling efforts were on dabbling ducks of the genera Anas, Aix, Cairina, and Dendrocygna because of their previously documented role as hosts of AIV, especially H5 and H7. Each state attempted to collect 200 samples per

species or functional group and focused 70% of their efforts during migration periods (USDA, 2006).

The US Strategic Plan (USDA, 2006) identified species from the genera *Aythya*, *Bucephala*, *Clangula*, *Histrionicus*, *Lophodytes*, *Melanitta*, *Mergus*, *Oxyura*, *Polysticta*, and *Somateria* as the diving duck functional group. Genera included in the geese and swans functional group were: *Anser*, *Branta*, *Chen*, and *Cygnus*. Species from the genera *Actitis*, *Aphriza*, *Arenaria*, *Bartramia*, *Calidris*, *Charadrius*, *Gallinago*, *Haematopus*, *Himantopus*, *Limnodromus*, *Limosa*, *Numenius*, *Phalaropus*, *Pluvialis*, *Recurvirostra*, *Scolopax*, *Tringa*, and *Tryngites* were categorized as shorebirds. Genera included in the gulls and terns functional group were: *Aethia*, *Alca*, *Alle*, *Anous*, *Brachyramphus*, *Cepphus*, *Chlidonias*, *Fratercula*, *Gelochelidon*, *Hydroprogne*, *Larus*, *Onychoprion*, *Ptychoramphus*, *Rhodostethia*, *Rhynchops*, *Rissa*, *Sterna*, *Synthliboramphus*, *Thalasseus*, and *Uria*. The final functional group, other water birds, included genera such as *Ardeidae*, *Diomedidae*, *Gaviidae*, *Gruidae*, *Podicipedidae*, *Procellariidae*, and *Rallidae*.

We accessed the USDA-APHIS-WS database to import surveillance data into an Access database (Microsoft Office, 2007) to query positive results of rRT-PCR matrix assays. We used the frequency procedure in SAS 9.2 ([PROC FREQ]; SAS Institute, 2008) to perform chi-square tests to determine differences ($\alpha = 0.05$) among all 4 flyways for 2007–2009 and to determine differences ($\alpha = 0.05$) in apparent prevalence of AIV among years for the same flyway. We used the Fisher's Exact Test (Fisher, 1925) to determine differences ($\alpha = 0.05$) in apparent prevalence between flyways if we detected differences with chi-square tests. The Fisher's Exact Test is appropriate for comparisons between 2 groups (1 degree of freedom) or for sample sizes < 5 (Fisher, 1925). We

calculated exact binomial 95% confidence intervals for all apparent prevalences (Clopper and Pearson, 1934). All estimates of prevalence we report are apparent and throughout the paper we will refer to apparent prevalence as prevalence.

We also developed 32 candidate generalized linear mixed models (GLMM; Appendix A) to explain AIV prevalence from 2007 to 2009 and validate the results of our descriptive statistics. We used mixed models to incorporate a random intercept in all models. We selected latitude (Lat) as the random effect to allow model intercepts to account for latitudinal variation in prevalence of AIV. All possible combinations of 4 fixed effects including month, flyway (FW), year, and functional group (FG) were evaluated. We evaluated pair-wise interaction models of fixed effects. We used R 2.12.2 (R Core Development Team, 2008) to fit candidate models. We adjusted month to coincide with the beginning of our biological year (April 1) for the input and adjusted the results back. We included a smoothing term to the month parameter to improve convergence. We evaluated all candidate models using Bayesian Information Criterion ([BIC]; Schwarz, 1978) rather than Akaike Information Criterion ([AIC]; Akaike, 1974) because AIC may over fit more complex models based on number of parameters and give them more weight (Burnham and Anderson, 2002). We also calculated the area under the receiver operation characteristic curve (AUC) to measure the discriminatory power of the model (Fielding, 1997; Danks and Porter, 2008). The AUC scores range from 0.5 (no better than random) to 1.0 (best possible fit; Hosmer and Lemeshow, 2000).

We calculated monthly prevalence of AIV for all flyways, 2007–2009, and plotted them to determine peaks in prevalence. We defined the spring migration period as January–June and the fall migration period as July–December. Waterfowl migration varies greatly by species. The blue-winged teal (*Anas discors*) is among the earliest to leave the breeding grounds of southern Canada and the prairie pothole region of North and South Dakota and arrive on wintering areas in Florida, Louisiana and Texas as early as September (Bellrose, 1976). Canada geese (*Branta canadensis*) may begin northward migrations in the spring as early as mid January, depending on conditions (Bellrose, 1976). We used the regression procedure in SAS 9.2 ([PROC REG]; SAS Institute, 2008) to conduct a linear regression to test for correlation between prevalence and sample size.

RESULTS

Sampling distribution

Samples were collected in all 4 flyways throughout 2007–2009. Total samples collected were 61,115 in 2007, 63,378 in 2008, and 44,447 in 2009 (Figure 3-2). The Atlantic Flyway had the highest proportion of samples collected each year (range = 30%–33%). The Mississippi Flyway had the second highest proportion of samples (range = 26%–28%), followed by the Central (range = 21%–23%), and Pacific (20%) Flyways. The majority of sampling was conducted in the July–December in all flyways: Atlantic (64%), Mississippi (68%), Central (89%), and Pacific (82%). Hunter harvested birds constituted 69% of samples, live wild birds were 28%, and mortality/morbidity investigations were 1% of total samples. Regression analysis found little correlation between sample size and prevalence ($R^2 = 0.07$).

Flyway prevalence

Prevalence differed among flyways in all years (2007–2009; $\chi^2 = 433.4$, 237.1, 454.2; P < 0.001; Figure 3-3). We found differences ($P \le 0.016$) in prevalence of AIV between all flyways in 2007–2009. In the Atlantic Flyway, we found differences in prevalence of AIV among and between the sampling periods, 2007–2009 ($\chi^2 = 36.71$; *P* < 0.001). In the Mississippi and Central Flyways, differences in prevalence of AIV was detected among sampling periods ($\chi^2 = 333.6$, 49.41, respectively; *P* < 0.001) and between sampling periods (*P* < 0.001 and *P* ≤ 0.019, respectively). In the Pacific Flyway no differences ($\chi^2 = 1.885$; *P* = 0.390) in prevalence of AIV were detected among years.

Generalized linear mixed model analysis

The best-fit model carried 100% of the weight and included the parameters: FW, FG, month, year, the interactions of FG and month, FW and month, and FW and year, with the random effect Lat.. The second-best model was the global model with < 0.001% weight (Table 3-1). The global and null models are included in the table for structural comparison. The calculated AUC for best-fit model was 0.69 (Figure 3-4), indicating an adaquate fit to the data. The intercept estimate for the best-fit model represents the Atlantic Flyway, dabbling duck functional group, late October, and 2007. Estimates indicated that AIV was higher in the dabbling duck functional group than all other functional groups. The effect of the interaction of month and functional group was significant (P <0.001) and results suggested that AIV declined in dabbling ducks after late October. Prevalence of AIV was higher 2008 than 2007 and higher in 2009 than in 2007 or 2008. We detected differences approaching significance in prevalence between the Atlantic and Central Flyways (P = 0.066; Table 3-2) and descriptive statistics we calculated detected differences (P < 0.001) in all years.

Timing

Atlantic Flyway. In the Atlantic Flyway, 34,268 samples (64%) were collected during the fall migration period. We detected peaks in prevalence of AIV in September 2007,

September 2008, and October 2009 (Figure 3-5). In 2007, 88% of all positive samples (n = 212) were from dabbling ducks which made up 80% of total samples that month. In 2008, 96% of all positive samples (n = 437) were from dabbling ducks and constituted 84% of total samples collected that month. In October 2009, nearly all positive samples (97%) were in dabbling ducks. Dabbling ducks made up 74% of the total collections while shorebirds made up 11% and had no positives.

Thirty-six percent of samples (n = 19,517) were collected during the spring sampling period. Peaks occurred in May 2008 and May 2009. Peaks were detected concurrent with sampling at the Delaware Bay area located between Delaware and New Jersey. In 2008, 96% of all positives (n = 80) were from the shorebird functional group, specifically 74 ruddy turnstones (*Arenaria interpres*), and 1 positive was detected in a Canada goose (*Branta canadensis*). Shorebird samples consisted of 47% of the total while geese and swans consisted of 40% of the total samples collected. In 2009, all 51 positive samples in May were collected from ruddy turnstones. Shorebirds were 53% of the total sample and geese and swans were 34% of the total sample. A peak in AIV occurred in February 2010, with 85% of all positives (n = 140) occurring in dabbling ducks and 14% occurring in geese and swans. Dabbling ducks constituted 43% of total collections, geese and swans constituted 34% of total collections, and diving ducks constituted 22% of total collections for that month.

Mississippi Flyway. In the Mississippi Flyway, 32,993 samples were collected during the fall sampling period. Peaks in prevalence of AIV were earlier than the Atlantic Flyway and occurred in August–November yearly (Figure 3-6). In September 2007, 94% of all positive samples (n = 155) occurred in dabbling ducks. Dabblers made up 89% of the

total collection that month and geese and swan collection was 8% of the total. In August 2008, 91% of all positive samples (n = 128) were from dabbling ducks and 7% of positive samples were from diving ducks. Dabblers made up 79% and divers made up 13% of the total samples in August 2008. In August 2009, 93% of all positive samples (n = 150) were collected from dabbling ducks. Dabbling ducks made up 86% and geese and swans made up 9% of the total samples for that month.

Thirty-two percent of samples (n = 15,640) were collected during the spring sampling period. In February 2009, 69% of all positive samples (n = 42) occurred in geese and swans and 31% occurred in dabbling ducks. Geese and swans made up 39% of the total sample while dabbling ducks made up 61% of the total sample for the month. In March 2010, 96% of all positive samples (n = 56) were in dabbling ducks and 4% of positive samples were collected from geese and swans. Dabbling ducks were 32% of all samples and geese and swans were 60% of samples.

Central Flyway. In the Central Flyway, 32,187 samples (89%) were collected during the fall sampling period. All fall peaks in prevalence of AIV in the Central Flyway occurred in August (Figure 3-7). The peaks in prevalence of AIV observed in August in the Central Flyway were higher than observed in the other flyways. In 2007, 98% of all positive samples (n = 327) were collected from dabbling ducks but they were only 79% of the sample collected in August. Shorebirds constituted 14% of birds sampled with only 1 positive in a least sandpiper (*Calidris minutilla*). In August 2008, 96% of all positive samples (n = 210) were collected from dabbling ducks. Eighty-six percent of samples collected that month were dabbling ducks and 11% of samples were collected from shorebirds. No positive shorebird samples were collected. In August 2009, 96% of all

positive samples (n = 178) were collected from dabbling ducks and the remaining 4% of positives were collected from diving ducks. Dabblers made up 84% of the total sample while divers made up 10% of the total sample during that period.

Eleven percent of samples (n = 4,069) were collected during the spring sampling period. Spring peaks in prevalence of AIV occurred in February 2009 and March 2010. In February 2009, 92% of all positive samples (n = 40) were collected from dabbling ducks and the remaining 8% of positive samples were collected from geese and swans. Dabblers constituted 55% and geese and swans constituted 42% of the total sample for the month. In March 2010, dabbling ducks were 78% of all positives (n = 18) and geese and swans were the remaining 22% of positives. Dabblers made up 62% and geese and swans made up 38% of the total sample that month.

Pacific Flyway. In the Pacific Flyway, 27,654 of samples (82%) were collected during the fall sampling period. We detected peaks in prevalence of AIV in July–November yearly (Figure 3-8). In August 2007, 99% of all positive samples (n = 422) were collected from dabbling ducks. Dabblers made up 87% of the total sample that month. In October 2007, 98% of all positive samples (n = 436) were collected from dabbling ducks. Dabblers made up 84% of the total sample that month and geese and swans made up 13% of the total sample. Geese and swans only constituted 1% of positive samples that month. In August 2008, 99% of all positive samples (n = 457) were collected from dabbling ducks. Dabblers made up 94% of the total samples collected and shorebirds made up 4% of samples. In September 2009, 99% of all positive samples (n = 158) were collected from dabbling ducks. Dabblers constituted 93% of the total sample for the month. In December 2009, 70% of all positive samples (n = 139) were collected from the month. In December 2009, 70% of all positive samples (n = 139) were collected from the month. In December 2009, 70% of all positive samples (n = 139) were collected from the month. In December 2009, 70% of all positive samples (n = 139) were collected from the month. In December 2009, 70% of all positive samples (n = 139) were collected from the month. In December 2009, 70% of all positive samples (n = 139) were collected from the month. In December 2009, 70% of all positive samples (n = 139) were collected from the month. In December 2009, 70% of all positive samples (n = 139) were collected from the month. In December 2009, 70% of all positive samples (n = 139) were collected from the month. In December 2009, 70% of all positive samples (n = 139) were collected from the month. In December 2009, 70% of all positive samples (n = 139) were collected from the month.

dabbling ducks and 24% were collected from geese and swans. Dabblers constituted 80% of the total sample and geese and swans constituted 15% of the total sample for the month. Eighteen percent of samples (n = 6,120) were collected during the spring sampling period. Minor peaks occurred in March 2008 and 2009 however, positive samples for both months were 1 and 2, respectively.

DISCUSSION

Prevalence was lowest each year in the Atlantic Flyway but sample sizes were highest. North American waterfowl, shorebirds, gulls, and terns are known to migrate to Iceland, Greenland, and Western Europe (Tuck, 1971; Edgell, 1984; Boertmann et al., 2004). These movements may lead to contact between North American birds and birds from HPAIV endemic areas of Europe. We found high prevalence during spring in shorebirds at Delaware Bay, an important migratory stop-over, but if mixing with Eurasian birds is the mechanism for the spread of HPAIV to North America, spring sampling of birds on northward migrations would not yield HPAIV. We suggest sampling in the Atlantic Flyway be concentrated in August–October as our research showed highest peaks in prevalence and spring sampling be discontinued.

The Mississippi Flyway had the second greatest sampling effort with ranges of prevalence of AIV similar to those in the Central Flyway. Our results suggest that while sampling is important in the Mississippi Flyway, due to mixing of birds that use areas of Alaska (Lincoln, 1935), a portion of sampling effort could be shifted to Central or Pacific Flyways due to higher estimated prevalences in the western flyways. We suggest sampling effort be concentrated in August–November as prevalence was highest during those periods but sampling effort was often initially low. Cloacal and tracheal swabs were collected from 1,389 dabbling ducks for AIV surveillance in coastal Louisiana during September–January in 1986–1987 and prevalence of AIV decreased from 3.1% to 0.4% during the study period (Stallknecht et al., 1990). Our results for the same time period showed higher prevalence of AIV, but birds in our study were collected from a larger area and if mixing or migrations are rare, local prevalence may be much lower.

The third highest sampling effort was in the Central Flyway. We suggest surveillance effort should be increased in July and August, where migratory birds are abundant, because we observed peaks in parvalence yearly, but sampling effort was relatively low. Sampling effort was high in September concurrent with early teal seasons and abundant hunter harvest samples, but peak of AIV infection of waterfowl may be missed at this time. Our calculated prevalence for August was 23%–35%. Similar numbers of AHY (1,046) and HY (1,208) birds were collected, so we didn't expect bias in prevalence due to a larger sample of HY birds. Prevalence of AIV in live, hatch-year ducks, sampled with cloacal swabs only, in the Central Flyway of Canada in August and September 2005 revealed prevalence of 10% (Parmley et al., 2008). Prevalence of AIV in dabbling ducks in Minnesota was estimated at 11% from cloacal swabs collected in September 1998–2000 (Hanson et al., 2003). Cloacal swabs collected from 258 live dabbling ducks in February 2001, August 2002, and February 2002 along the Gulf Coast of Texas revealed prevalences of 11%, 0% and 15%, respectively (Hanson et al., 2005). Prevalence of AIV in February in our study ranged from 1% to 14% with similar sample sizes ($\overline{x} = 219$). Cloacal only sampling in the previous studies likely led to lower AIV prevalence than we report because some subtypes of AIV can be shed orally (Sturm-Ramirez et al., 2005). In addition, prevalence of AIV in dabbling ducks (6%) was higher than in diving ducks (2%) in 1,415 hunter-harvested ducks collected from the Gulf Coast

of Texas in November, 2005–Janurary, 2006 (Ferro et al., 2008). We reported similar estimates (6%) for all birds collected in the same months in 2007–2009.

The Pacific Flyway had the fewest number of samples collected each year yet prevalence was highest among the 4 flyways in 2007 and 2008. This was the only flyway that had consistant prevalence of AIV among years (~13%). Birds in the Pacific Flyway may have previous exposure to a greater number of subtypes of AIV, thus flock immunity. In Alaska, 45% of LPAIV viruses from northern pintails (Anas acuta) had gene segments more closely related to Asian strains than North American strains (Koehler et al., 2008). Wahlgren et al. (2008) described isolation of H6N1 from a Dunlin (*Calidris alpina*) collected in Alaska that had gene segments more closely related to Asian lineages of AIV than North American lineages of AIV. Surveillance of domestic ducks in South Korea discovered H3N2 AIV that was more closely related to the North American strain than the Eurasian strain (Kang et al., 2009). An increase in total samples is suggested for the Pacific Flyway, especially at the Alaskan interface becasue the Alaska-East Asia pathway is suspected as the most likely route for HPAIV introduction into North America from migratory birds (DeLiberto et al., 2009). As with the Mississippi and Central Flyways, we suggest an increased sampling effort in August– October in the Pacific Flyway. Prevalence peaked in August in 2007 and 2008 so increased sampling is warranted and we also detected a peak in December, 2009, which was later than the previous two years. Parmley et al. (2008) reported 55% prevalence of AIV in live, hatch-year dabbling and diving ducks collected in August and September in the Pacific Flyway of Canada. Collection of hatch-year only birds may have led to higher prevalence than we report. If HPAIV H5N1 spreads into northeastern Siberia, including

Wrangel Island, then the risk of introduction of H5N1 into North America by migratory birds will increase substantially (Kilpatrick et al., 2006).

Results of our mixed model analysis confirmed results of our descriptive statistics. The best fit-model confirmed our previous findings that prevalence of AIV was higher in dabbling ducks than other functional groups and prevalence increased yearly from 2007 to 2009. Perhaps the most significant finding of our generalized linear mixed model analysis was the optimal time for sampling. Future surveillance efforts should be focused on the fall migration period before late October for dabbling ducks. This supports our previous analyses suggesting surveillance efforts should focus on August–October. Model estimates also indicated diving ducks and geese and swans had higher prevalence after late October, so sampling of those functional groups should take place during the remainder of the fall migration period in November and December.

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Table 3-1. Results of the generalized linear mixed model (GLMM) analysis of avian influenza virus infection in samples collected from migratory birds collected in the US, 2007–2009.

Model	Explanatory variables	k	BIC	Δ BIC	weight	AUC
Best- fit	FW + FG + Month + Year +	36	104,379	0	1	0.69
	FW*Month + FG*Month +					
	Year*FW + Lat					
Global	FW + FG + Month + Year +	46	104,430	51	< 0.001	-
	FW*Month + FG*Month +					
	Year*FW + FG*Year + Lat					
Null	1 + Year + Lat	4	110,544	6164	0	-

PN = positive/negative avian influenza infection, FW = flyway (Atlantic, Mississippi, Central, Pacific), FG = functional group (dabbling duck, diving duck, geese and swan, shorebird, gull and tern, other water bird), Lat = latitude (24°–68° N), * = interaction of 2 parameters, BIC = Bayesian Information Criterion, AUC = area under the receiver operating curve predicting the fit of the model

Table 3-2. Estimates and *P* values from the best-fit model PN ~ FW + FG + Month + Year + FW*Month + FG*Month + Year*FW + Lat that describes avian influenza virus infection in samples collected from migratory birds in the US, 2007–2009.

Coefficient	Estimate	Std. Error	z value	<i>P</i> (> z)	
Intercept ¹	-2.6373	0.1349	-19.549	< 0.0001	
FWC	0.0853	0.0464	1.837	0.0662	
FWM	0.1504	0.0447	3.362	0.0008	
FWP	0.5220	0.0456	11.469	< 0.0001	
FGdiv	-1.0930	0.0511	-21.396	< 0.0001	
FGgs	-1.6924	0.0518	-26.415	< 0.0001	
FGgt	-0.6146	0.1019	-6.031	< 0.0001	
FGo	-1.5308	0.2751	-5.564	< 0.0001	
FGsb	-2.6684	0.1744	-15.302	< 0.0001	
Month	-0.1794	0.0221	-8.110	< 0.0001	
Year2008	0.2692	0.0391	6.880	< 0.0001	
Year2009	0.3227	0.0452	7.143	< 0.0001	
FWC*Month	-0.3342	0.0332	-10.072	< 0.0001	
FWM*Month	0.1550	0.0302	5.130	< 0.0001	
FWP*Month	-0.3725	0.0332	-11.232	< 0.0001	
FGdiv*Month	0.4710	0.0635	7.417	< 0.0001	
FGgs*Month	0.6055	0.0331	18.309	< 0.0001	
FGgt*Month	-0.4341	0.1168	-3.717	0.0002	

Coefficient	Estimate	Std. Error	z value	<i>P</i> (> z)
FGo*Month	1.1912	0.3815	3.122	0.0018
FGsb*Month	-0.3587	0.1941	-1.848	0.0646
FWC*2008	-0.0834	0.0564	-1.480	0.1388
FWM*2008	0.0242	0.0544	0.444	0.6569
FWP*2008	-0.2676	0.0552	-4.850	< 0.0001
FWC*2009	-0.0114	0.0620	-0.184	0.8543
FWM*2009	0.2737	0.0593	4.613	< 0.0001
FWP*2009	-0.3726	0.0625	-5.959	< 0.0001

PN = positive/negative avian influenza infection, FW = flyway (A = Atlantic, C =

Central, M = Mississippi, P = Pacific), FG = functional group (dab = dabbling ducks, div

= diving ducks, gs = geese and swans, gt = gulls and terns, o = other water birds, sb =

shorebirds), Lat = lat $(24^{\circ}-68^{\circ} \text{ N})$, * = interaction of 2 parameters

¹ The intercept included the parameters for the Atlantic Flyway, dabbling duck functional group, late October, and 2007.


Figure 3-1. The major migratory bird flyways of the US (Lincoln, 1935).



Figure 3-2. Number of samples collected for highly-pathogenic avian influenza surveillance by North American migratory bird flyway and year (2007–2009).



Figure 3-3. Prevalence of avian influenza virus by North American migratory bird flyway, 2007–2009 (n = 168,940).



Figure 3-4. The area under the curve (AUC) of the receiver operating curve predicting the fit of the best-fit model: PN ~ FW + FG + Month + Year + FW*Month + FG*Month + Year*FW + Lat, that addresses prevalence of avian influenza virus in sampled birds in the US, 2007–2009.

PN = positive/negative avian influenza infection, FW = flyway, FG = functional group, Lat = lat, * = interaction of 2 parameters.



Figure 3-5. Prevalence of avian influenza virus and sampling effort by month in the Atlantic Flyway of the US, 2007-2009 (n = 76,524).



Figure 3-6. Prevalence of avian influenza virus and sampling effort by month in the Mississippi Flyway of the US, 2007-2009 (n = 64,929).



Figure 3-7. Prevalence of avian influenza virus and sampling effort by month in the Central Flyway of the US, 2007-2009 (n = 52,384).



Figure 3-8. Prevalence of avian influenza virus and sampling effort by month in the Pacific Flyway of the US, 2007-2009 (n = 49,248).

Appendix A. Summary list of 32 generalized linear mixed models (GLMM) used for analysis of avian influenza virus infection in samples collected from migratory birds in the US, 2007–2009.

- 1) $PN \sim 1 + Year + Lat$
- 2) $PN \sim FW + Year + Lat$
- 3) $PN \sim FG + Year + Lat$
- 4) $PN \sim FW + FG + Year + Lat$
- 5) $PN \sim Month + Year + Lat$
- 6) $PN \sim FW + Month + Year + Lat$
- 7) $PN \sim FG + Month + Year + Lat$
- 8) $PN \sim FW + FG + Month + Year + Lat$
- 9) $PN \sim FW + Month + Year + Year*FW + Lat$
- 10) $PN \sim FW + FG + Month + Year + Year * FW + Lat$
- 11) $PN \sim FG + Month + Year + FG*Month + Lat$
- 12) $PN \sim FW + FG + Month + Year + FG*Month + Lat$
- 13) $PN \sim FW + FG + Year + FG^*FW + Lat$
- 14) $PN \sim FW + FG + (Month + Year + FG*FW + Lat)$
- 15) $PN \sim FW + Month + Year + FW*Month + Lat$
- 16) $PN \sim FW + FG + Month + Year + FW*Month + Lat$
- 17) PN ~ FW + FG + Month + fYear + FW*Month + FG*Month + Lat
- 18) $PN \sim FW + Month + Year + FW*Month + Year*FW + Lat$
- 19) $PN \sim FW + FG + Month + Year + FW*Month + Year*FW + Lat$
- 20) PN ~ FW + FG + Month + Year + FW*Month + FG*Month + Year*FW + Lat

- 21) $PN \sim FW + FG + Year + FG^*Year + Lat$
- 22) $PN \sim FG + Month + Year + FG*Year + Lat$
- 23) $PN \sim FW + FG + Month + Year + FG*Year + Lat$
- 24) $PN \sim FW + FG + Year + Year*FW + FG*Year + Lat$
- 25) $PN \sim FW + FG + Month + Year + Year*FW + FG*Year + Lat$
- 26) $PN \sim FG + Month + Year + FG*Month + FG*Year + Lat$
- 27) $PN \sim FW + FG + Month + Year + FG*Month + FG*Year + Lat$
- 28) $PN \sim FW + FG + Month + Year + FG^*FW + FG^*Year + Lat$
- 29) PN ~ FW + FG + Month + Year + FW*Month + FG*Year + Lat
- 30) PN ~ FW + FG + Month + Year + FW*Month + FG*Month + FG*Year + Lat
- 31) PN ~ FW + FG + Month + Year + FW*Month + Year*FW + FG*Year + Lat
- 32) PN ~ FW + FG + Month + Year + FW*Month + FG*Month + Year*FW +

FG*Year + Lat

PN = positive/negative avian influenza infection, FW = flyway, FG = functional group, Lat = lat, * = interaction of 2 parameters.

CHAPTER 4: AVIAN INFLUENZA VIRUS PREVALENCE IN MIGRATORY BIRDS BY FUNCTIONAL GROUP AND SPECIES IN THE UNITED STATES, 2007–2009

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Abstract: Highly-pathogenic avian influenza virus (HPAIV) H5N1 poses risks to wild birds, poultry, and humans. The US Department of Agriculture-Animal Plant Health Inspection Service-Wildlife Services (USDA-APHIS-WS), state, and tribal wildlife agencies collected 168,940 migratory birds from 2007 to 2009 as part of an interagency early detection system for HPAIV. Migratory birds from 6 functional groups (i.e., dabbling ducks, diving ducks, geese and swans, shorebirdss, gulls and terns, and other water birds) were collected. No HPAIV was found, but combinations of the 16 hemagglutinin (H) and 9 neuraminidase (N) subtypes of low-pathogenic avian influenza viruses (LPAIV) were discovered, including H5 and H7 subtypes. Dabbling ducks had higher prevalence of AIV ($\bar{x} = 14.1\%$; range = 9.3%–19.4%; *P* < 0.001) than other functional groups across all flyways and study years. The species with high prevalence of AIV were: American green-winged teal (*Anas creeca*, range = 9%–22%), blue-winged teal (*A. discors*, range = 8%-22%), mallard (*A. platyrhynchos*, range = 12%-27%), northern pintail (*A. acuta*, range = 3%-28%), and northern shoveler (*A. clypeata*, range = 4%-21%). These species also were most often sampled by participating agencies. Our results suggest future surveillance of AIV should focus on species from the dabbling duck functional group.

Key words: avian influenza virus, dabbling ducks, disease surveillance, highlypathogenic, waterfowl

Abbreviations: AIC = Akaike's Information Criterion, AIV = avian influenza virus, , AUC = area under the receiver operating curve, BIC = Bayesian Information Criterion, FG = functional group, FW = flyway, GLMM = generalized linear mixed model, H = hemagglutinin, HPAIV = highly-pathogenic avian influenza virus, Lat = latitude, LPAIV = low-pathogenic avian influenza virus, N = neuraminidase, PN = positive/negative avian influenza infection, PROC FREQ = frequency procedure, ROC = receiver operating curve, rRT-PCR = real-time reverse transcriptase polymerase chain reaction, SAS = Statistical Analysis Software, USDA-APHIS-WS = US Department of Agriculture-Animal Plant Health Inspection Service-Wildlife Services

INTRODUCTION

Wild waterfowl are the primary reservoir and an important long-term evolutionary source for influenza A viruses (Sturm-Ramirez et al., 2005). Influenza A viruses of 16 hemagglutinin (H) and 9 neuraminidase (N) combinations are typically non-pathogenic and cause natural infections in wild birds; only the H5 and H7 subtypes have caused HPAIV in avian species (Alexander, 2000; Olsen et al., 2006). Influenza viruses have been isolated in 13 orders of birds, but mostly in *Anseriformes* and *Charadriiformes* (Stallknecht and Shane, 1988; Gilbert et al., 2006). Species in these orders are thought to

be particularly susceptible because they are exposed to shallow water that may be contaminated with infected fecal or oral material, especially during fall congregations (Sturm-Ramirez et al., 2005; Rappole and Hubalek, 2006). Species from the family Anatidae pose the highest risk for transmission to other waterfowl and domestic poultry because they may excrete large amounts of virus and remain healthy while moving large distances (Delogu et al., 2003; Hulse-Post et al., 2005; Gaidet et al., 2010). Concern has been raised about the role wild birds play in harboring, perpetuating, and transmitting AIV to new geographic locations, internationally and intercontinentally (Guberti and Newman, 2007; Boyce et al., 2009). Highly-pathogenic AIVs evolve in domestic poultry from low-pathogenic avian influenza viruses (LPAIV) that circulate widely in birds (Webster et al., 1992; Alexander et al., 1993). Different influenza subtypes also can infect ducks concomitantly, creating the opportunity for genetic mixing (Sharp et al., 1997). Low-pathogenic AIVs cause mild respiratory diseases that may be exacerbated by other infections or extreme environmental conditions (Alexander, 2000). Clinical signs of HPAIV H5N1 infection in waterfowl include paralysis, unusual head tilt, staggering, and death (Chen et al., 2005).

Migration of waterfowl in North America generally follows 4 major flyways: the Atlantic, Mississippi, Central, and Pacific (Lincoln, 1935; Figure 4-1). Alaska and the Pacific Flyway are thought to be the most likely points of introduction of wild waterfowl infected with HPAIV to North America because of proximity to Siberia and the East Asia Flyway (DeLiberto et al., 2009). Three pathways are used annually by waterfowl between hemispheres: Alaska–East Asia, East Asia–Pacific North America and Europe–Atlantic North America (Rappole and Hubalek, 2006). Given that migratory birds pose a risk of HPAIV entry into the US, surveillance in areas where intercontinental migrants enter the country, such as Alaska, may yield the first evidence of introduction (US Department of Agriculture, [USDA] 2006; DeLiberto et al., 2009). Thirty-three species of waterfowl, 46 species of shorebirds, and 15 species of gulls and terns equaling an estimated 1.5–2.9 million individuals move from Asia to North America and vice versa each year (Winker and Gibson, 2010). Satellite telemetry data from migrating northern pintails revealed crossover between Alaska and Russia (Miller et al., 2005). Genetic analyses of AIVs suggest that exchange of viruses between Eurasian and American clades does not occur frequently and introduction of HPAIV to North America by migratory birds would be unlikely via the Alaska–East Asia pathway (Webster et al., 1992; Olsen et al., 2006; Krauss et al., 2007). Conversely, a study of LPAIV in northern pintails in Alaska found 45% of viruses had gene segments more closely related to Asian strains than North American strains (Koehler et al., 2008) and isolation of H6N1 from a Dunlin (Calidris *alpina*) collected in Alaska revealed gene segments more closely related to Asian lineages of AIV than North American lineages of AIV (Wahlgren et al., 2008). Surveillance for AIV in domestic ducks in South Korea discovered H3N2 AIV that was more closely related to the North American strain than the Eurasian strain (Kang et al., 2009). In India, H11N1 was isolated from surveillance of live wild birds (Pawar et al., 2010). The authors found that the virus was related to AIV isolated in shorebirds in Delaware, US, in 2000 and 2003. An American wigeon (Anas americana) collected in Sonora, Mexico was infected with H9 AIV that was more closely related to Eurasian than North American isolates (Montalvo-Corral and Hernandez, 2010). The H5 subtype is uncommon in migratory birds in North America and was detected in only 555 of 145,055

samples collected from 2006 to 2008 ([0.4%]; DeLiberto et al., 2009; Pedersen et al., 2010). Ninety-one percent of H5 detections in North America were from dabbling ducks and 48% were found in mallards (Pedersen et al., 2010).

Waterfowl commonly congregate in permanent wetlands with dense emergent vegetation after breeding where juveniles mature, adults molt, and species mix before migration, which leads to increased risk of spreading AIV (Gilbert et al., 2006). The best opportunities for viral transmission among large numbers of Anseriformes hosts may be on lakes and ponds in summer where large concentrations of birds gather for weeks to undergo the post-breeding, pre-migratory molt (Webster et al., 1992). Congregations of waterfowl may lead to high prevalence of AI in naïve juveniles just before fall migrations (Fouchier et al., 2007; Webster et al., 2007; Munster and Fouchier, 2009). Prevelance of AIV declines on wintering grounds as immunity of flocks build (Halvorson et al., 1985; Munster et al., 2007; Wallensten et al., 2007). Pink-footed geese (Anser brachyrhynchus) had higher prevalence of AIV (63%) in November–January on their over-wintering location than at any other time or location ([0%]; Hoye et al., 2011) and prevalence of AIV as high as 9.5% was reported in mallards in March–June (Wallensten et al., 2007). Eighty-eight percent of positive samples for AIV in Iran were collected in February and March (Ferdidouni et al., 2010).

Survival of AIVs outside hosts is affected by humidity, ultraviolet radiation, water salinity, and temperature (Brown et al., 2007; Weber and Stilianakis, 2008; Shahid et al., 2009; Zuk et al., 2009). Estimated survival duration of HPAIV H5N1 acquired from poultry in Korea was 930–3,213 days in 4°C water (Paek et al., 2010). Persistence of HPAIV H5N1 was longer (> 60 days) at 4°C water than in 20°C water ([14–21 days]; Domanska-Blicharz et al., 2010). Survival of HPAIV H5N1 was 350 days in -10°C water while survival was only 13 days in 30°C water (Nazir et al., 2010). Eight H5 and H7 LPAIVs persisted for 128–375 days and 2 HPAIV H5N1 persisted for 82–182 days in 17°C water while those same LPAIVs and HPAIVs persisted for 19–61 days and 28 days in 28°C water, respectively (Brown et al., 2007). Survival of AIVs in water suggests the possibility of an environmental reservoir, but rapid loss of infectivity has been observed in freeze-thaw experiments (Stallknecht et al., 2010). Outbreaks in wild birds may be associated with periods of environmental or physiological stress (Globig et al., 2009). Avian influenza infection in migratory birds can vary greatly according to season and location because species exhibit different migratory behaviors, habitat preferences, and geographic ranges (Stallknecht and Brown, 2007). Timing relative to migration is the determinant of prevalence of influenza A virus (Munster and Fouchier, 2009).

Important migratory stop-over areas such as the Rainwater Basin of Nebraska hold potential for concentrating waterfowl and shorebirds, leading to virus transmission. In the spring of 2001, an estimated 7.2 million lesser snow geese (*Chen caerulescens*) and Ross's geese (*C. rossii*) were observed in the Rainwater Basin and Platte River Valley of Nebraska (Vrtiska and Sullivan, 2009). The Delaware Bay located between Delaware and New Jersey, in the Atlantic Flyway, concentrates nearly the entire population of red knots (*Calidris canutus*) during migration (Myers, 1986) and other species of shorebirds and waterfowl often exceeding 1 million individuals (Hanson et al., 2008). The Copper River Delta of Alaska, in the Pacific Flyway, has the largest spring concentrations of migratory shorebirds with up to 5 million birds per day (Bishop et al., 2000). Based on our knowledge of previous studies of LPAIV and HPAIV H5N1 outbreaks, we predicted members of the dabbling duck (especially *Anas*) and geese and swan (*Anser*, *Branta*, and *Cygnus*) functional groups would have the highest prevalence of AIV. The objectives of this study were to determine: 1) prevalence of AIV by functional group and species and 2) if differences existed among and between functional groups and species. Our results provide a comprehensive overview of AIV infection by functional group and species.

MATERIALS AND METHODS

Personnel with the USDA-Animal Plant Health Inspection Service-Wildlife Services (APHIS-WS) and state and tribal wildlife agencies collected samples from wild birds in all states for early detection of HPAIV in 2007–2009, using standardized protocols and procedures (USDA, 2006; DeLiberto et al., 2009; Pedersen et al., 2010). The USDA identified 5 collection strategies in the US Strategic Plan: live wild bird, sentinel, hunter harvest, morbidity/mortality investigation, and environmental sampling (USDA, 2006; DeLiberto et al., 2009). In 2007–2009, personnel collected cloacal and oropharyngeal samples from birds using sterile dacron-tipped swabs (Puritan, Puritan Medical Products LLC.) and combined them in vials containing 3 mL of brain-heart infusion broth (Becton Dickinson). Samples were kept cool, not frozen, and shipped to a National Animal Health Laboratory Network laboratory within 72 hours of collection (usually within 24 hours). We conducted sampling by biological year (April 1–March 31) from 2007 to 2009. Laboratory personnel screened samples for type A influenza with matrix real-time reverse transcriptase polymerase chain reaction (rRT-PCR) assays (Spackman, 2002) within 48 hours of receipt of samples. If a sample screened positive for H5 or H7, it was shipped to the National Veterinary Services Laboratory in Ames, IA for virus isolation, sub-typing, and pathogenicity testing. The US Strategic Plan (USDA, 2006) identified lists of migratory birds with potential exposure to HPAIV H5N1. The primary focus was on dabbling ducks of the genera *Anas*, *Aix*, *Cairina*, and *Dendrocygna* because of their previously documented role as hosts of AIV, especially H5 or H7. Each state attempted to collect 200 samples per species or functional group and focused 70% of their efforts during migration periods (UDSA, 2006).

The US Strategic Plan (USDA, 2006) identified species from the genera Aythya, Bucephala, Clangula, Histrionicus, Lophodytes, Melanitta, Mergus, Oxyura, Polysticta, and Somateria as the "diving duck" functional group. Genera included in the "geese and swans" functional group included Anser, Branta, Chen, and Cygnus. Species from the genera Actitis, Aphriza, Arenaria, Bartramia, Calidris, Charadrius, Gallinago, Haematopus, Himantopus, Linnodromus, Limosa, Numenius, Phalaropus, Pluvialis, Recurvirostra, Scolopax, Tringa, and Tryngites were categorized as "shorebirds." Genera included in the "gulls and terns" functional group were Aethia, Alca, Alle, Anous, Brachyramphus, Cepphus, Chlidonias, Fratercula, Gelochelidon, Hydroprogne, Larus, Onychoprion, Ptychoramphus, Rhodostethia, Rhynchops, Rissa, Sterna, Synthliboramphus, Thalasseus, and Uria. The final functional group "other water birds" included the families: Ardeidae, Diomedidae, Gaviidae, Gruidae, Podicipedidae, Procellariidae, and Rallidae.

We accessed the USDA-APHIS-WS database to import surveillance data into an Access database (Microsoft Office 2007) to query positive results of rRT-PCR matrix assays. We used the frequency procedure in SAS ([PROC FREQ]; SAS Institute, 2008)

to perform chi-square tests to determine differences ($\alpha = 0.05$) in apparent prevalence of AIV among all functional groups and all species within functional groups yearly for 2007–2009 for each flyway. We used the Fisher's Exact Tests in PROC FREQ in SAS (SAS Institute, 2008; Fisher, 1925) to determine differences ($\alpha = 0.05$) in apparent prevalence between 2 functional groups or 2 species within functional groups yearly. We did not make comparisons, either chi-square or Fisher's Exact, among or between years, only within a single biological year. We only performed the Fisher's Exact Test if differences were discovered with the chi-square test. The Fisher's Exact Test is appropriate for comparisons between 2 groups (1 degree of freedom) or for sample sizes < 5 (Fisher, 1925). We calculated exact binomial 95% confidence intervals for all estimates of apparent prevalence (Clopper and Pearson, 1934). We only considered a functional group or species for comparisons if it had a minimum of 10 positive samples to eliminate prevalences < 1% or to avoid inflated prevalences due to small sample sizes. All estimates of prevalence we report are apparent and throughout the paper we will refer to apparent prevalence as prevalence.

We developed 32 candidate generalized linear mixed models (GLMM; Appendix B) to explain AIV infection from 2007 to 2009 and validate the results of our descriptive statistics. We used mixed models to incorporate a random intercept in all models and selected latitude (Lat) as the random effect to allow model intercepts to account for latitudinal variation in prevalence of AIV. All possible combinations of 4 fixed effects including month, flyway (FW), year, and functional group (FG) were evaluated. We evaluated pair-wise interaction models of fixed effects using R 2.12.2 (R Core Development Team, 2008) to fit candidate models. We adjusted month to coincide with

the beginning of our biological year (April 1) and incorporated a smoothing term to month to improve convergence. We evaluated all candidate models using Bayesian Information Criterion ([BIC]; Schwarz, 1978) rather than Akaike Information Criterion ([AIC]; Akaike, 1974) because AIC may over fit more complex models based on number of parameters and give them more weight (Burnham and Anderson, 2002). We also calculated the area under the receiver operation characteristic curve (AUC) to measure the discriminatory power of the model (Fielding, 1997; Danks and Porter, 2008). The AUC scores can range from 0.5 (no better than random) to 1.0 ([best possible fit]; Hosmer and Lemeshow, 2000).

RESULTS

Functional Group

Atlantic Flyway. In 2007–2009, we found differences (P < 0.001) in prevalence of AIV among functional groups of migratory birds yearly ($\chi^2 = 266.7-499.9$). In all years dabbling ducks had higher prevalence of AIV than other functional groups (P < 0.001). Prevalence of AIV ranged from 9.3% to 11.9%, 3.1% to 4.9%, 2.3% to 3.8%, 4.6% to 7.3%, and 5.6% to 6.5% across years in dabbling ducks, diving ducks, geese and swans, gulls and terns, and shorebirds, respectively (Table 4-1).

In 2007, prevalence of AIV in dabbling ducks differed (P < 0.001) from all other groups tested. Diving ducks and geese and swans did not differ (P = 0.228), but we found differences between diving ducks and gulls and terns (P = 0.013) and diving ducks and shorebirds (P < 0.001). Geese and swans and gulls and terns did not differ (P = 0.115), but geese and swans differed (P = 0.001) from shorebirds. We found no differences (P =0.263) between gulls and terns and shorebirds (Table 4-1). In 2008, prevalence of AIV in dabbling ducks differed (P < 0.001) from all other groups. Diving ducks and geese and swans did not differ (P = 0.068), but diving ducks differed from both gulls and terns (P = 0.001) and shorebirds (P = 0.021). Geese and swans differed (P < 0.001) from gulls and terns, but shorebirds and gulls and terns did not differ (P = 0.461) from shorebirds. In 2009, we found differences (P < 0.001) in prevalence between all functional groups except for diving ducks and shorebirds (P =0.107; Table 4-1).

Mississippi Flyway. In 2007–2009, we found differences (P < 0.001) in prevalence of AIV among migratory bird functional groups yearly ($\chi^2 = 208.1-337.4$). In all years, dabbling ducks had higher prevalence of AIV than other functional groups (P < 0.001). Prevalence ranged from 11.1% to 19.4%, 3.9% to 11.1%, and 1.6% to 2.4% in dabbling ducks, diving ducks, and geese and swans, respectively, and was 5.5% in gulls and terms in 2008 (Table 4-2).

In 2007, differences existed (P < 0.001) between all functional groups. In 2008, dabbling ducks differed (P < 0.001) from all other functional groups. Diving ducks differed (P < 0.001) from geese and swans, and geese and swans differed (P < 0.001) from gulls and terns. Diving ducks and gulls and terns did not differ (P = 0.641). In 2009, we found differences (P < 0.001) between all functional groups (Table 4-1). *Central Flyway*. In 2007–2009, we discovered differences (P < 0.001) in prevalence of AIV among migratory bird functional groups yearly ($\chi^2 = 102.4-174.5$). In all years dabbling ducks had higher prevalence than other functional groups (P < 0.001). Prevalence of AIV ranged from 13.2% to 15.7%, 3.5% to 6.7%, 2.8% to 6.0%, in dabbling ducks, diving ducks, and geese and swans, respectively (Table 4-3). In 2007, dabbling ducks differed (P < 0.001) from the other functional groups. Diving ducks and geese and swans did not differ (P = 0.365). In 2008, dabbling ducks differed (P < 0.001) from other functional groups, but no differences (P = 0.379) were observed between diving ducks and geese and swans. In 2009, we found differences (P < 0.001) between all functional groups (Table 4-3).

Pacific Flyway. In 2007–2009, differences (P < 0.001) in prevalence of AIV existed among functional groups yearly ($\chi^2 = 69.4$ –195.2). Dabbling ducks had higher prevalence of AIV than other functional groups in all years (P < 0.001). Prevalence ranged from 14.5% to 16.1%, 3.6% to 7.9%, and 4.4% to 5.7% in dabbling ducks, diving ducks, and geese and swans, respectively (Table 4-4).

In 2007 dabbling ducks differed (P < 0.001) from other functional groups, but diving ducks and geese and swans did not differ (P = 0.113). In 2008, prevalence of AIV in dabbling ducks was different (P < 0.001) from the other functional groups but diving ducks and geese did not differ (P = 0.052). In 2009, differences in prevalence of AIV (P< 0.001) between dabbling ducks and diving ducks and dabbling ducks and geese and swans were significant. Diving ducks and geese and swans did not differ (P = 0.169; Table 4-4).

Species

Atlantic Flyway. In 2007, 9 species of dabbling ducks had adequate positive samples for comparison (see Appendix C for a complete list of dabbling ducks collected in all years and flyways and Appendix H for species to species comparisons of prevalence of AIV). We found differences in prevalence of AIV ($\chi^2 = 262.7$; P < 0.001) among American black duck ([ABDU]; *Anas rubripes*), American green-winged teal ([AGWT]; *A. crecca*),

blue-winged teal ([BWTE]; A. discors), gadwall ([GADW]; A. strepera), MALL, mottled duck ([MODU]; A. fulvigula), northern pintail (NOPI), northern shoveler ([NSHO]; A. clypeata), and wood duck ([WODU]; Aix sponsa; Figure 4-2). We found differences in prevalence of AIV among 4 species of diving ducks ($\chi^2 = 12.56$; P = 0.006; see Appendix D for a complete list of diving ducks collected in all years and flyways and Appendix I for species by species comparisons of prevalence of AIV): bufflehead ([BUFF]; Bucephala albeola), canvasback ([CANV]; Aythya valisineria), lesser scaup ([LESC]; A. affinis), and ring-necked duck ([RNDU]; A. collaris), 2 species of geese and swans (see Appendix E for a complete list of geese and swans collected in all years and flyways and Appendix J for species to species comparisons of prevalence of AIV), Canada geese ([CAGO]; Branta canadensis) and greater snow geese ([GSGO]; P < 0.001), and 4 species of shorebirds ($\gamma^2 = 37.36$; P < 0.001): red knot (REKN), ruddy turnstone ([RUTU]; Arenaria interpres), semi-palmated sandpiper ([SESA]; Calidris pusilla), and western sandpiper ([WESA]; C. mauri; Appendix G). We did not find a difference in prevalence ($\chi^2 = 0.8758$; P = 0.645) among 3 species of gulls and terns: common tern ([COTE]; Sterna hirundo), herring gull ([HERG]; Larus argentatus) and ring-billed gull ([RBGU]; L. delawarensis; Appendix F).

In 2008, 9 species of dabbling ducks had adequate positive samples for comparison. We found differences ($\chi^2 = 412.6$; *P* < 0.001) among ABDU, AGWT, AMWI, BWTE, MALL, MODU, NOPI, NSHO, and WODU (Figure 4-2). We found no differences ($\chi^2 = 7.20$; *P* = 0.066) in prevalence of AIV among 4 species of diving ducks: BUFF, LESC, RNDU, and ruddy duck ([RUDU]; *Oxyura jamaicensis*). We found differences ($\chi^2 = 428.3$, *P* < 0.001) among 3 species of geese and swans including: CAGO, GSGO, and mute swan ([MUSW]; *Cygnus olor*) and 2 species of gulls and terns, HERG and RBGU (P < 0.001).

In 2009, 9 species of dabbling ducks had an adequate number of positive samples for comparison. We detected differences ($\chi^2 = 152.2$; *P* < 0.001) in prevalence of AIV among ABDU, AGWT, AMWI, BWTE, MALL, mallard/black duck hybrid (MBDH), MODU, NOPI, and NSHO (Figure 4-2). We compared 2 species of diving ducks (i.e. BUFF and RNDU) and found no difference in prevalence (*P* = 0.255). We compared 3 species of geese, Atlantic brant ([ATBR]; *B. bernicla*), CAGO, and GSGO and found differences (*P* < 0.001) in prevalence among species ($\chi^2 = 57.7$). Only 1 shorebird (RUTU) had adequate positive samples so no interspecific comparisons were made within the functional group.

Mississippi Flyway. In 2007, we compared 9 species of dabbling ducks: ABDU, AGWT, AMWI, BWTE, GADW, MALL, NOPI, NSHO, and WODU and found differences ($\chi^2 = 242.8$; *P* < 0.001) among species (Figure 4-3). No other functional group had enough positive samples to include in comparisons.

In 2008, we compared 10 species of dabbling ducks: ABDU, AGWT, AMWI, BWTE, GADW, MALL, MODU, NOPI, NSHO, and WODU, and detected differences $(\chi^2 = 226.8; P < 0.0001)$ among species (Figure 4-3). We found differences $(\chi^2 = 12.16; P = 0.002)$ among 3 species of diving ducks: LESC, redhead ([REDH]; *A. Americana*), and RNDU. We also found differences (P < 0.001) in prevalence of AIV in 2 species of geese and swans: CAGO and lesser snow goose (LSGO).

In 2009, we compared 10 species of dabbling ducks. We found differences ($\chi^2 =$ 348.9; *P* < 0.001) among ABDU, AGWT, AMWI, BBWD, BWTE, GADW, MALL,

NOPI, NSHO, and WODU (Figure 4-3). We found differences ($\chi^2 = 22.5$; *P* < 0.001) among 4 species of diving ducks: BUFF, LESC, REDH, and RNDU. The CAGO was the only species with adequate positive samples from the geese and swans functional group, so no comparisons were made.

Central Flyway. In 2007, we compared 8 species of dabbling ducks: AGWT, AMWI, BWTE, GADW, MALL, NOPI, NSHO, and WODU, and found differences ($\chi^2 = 215.1$; P < 0.001) in prevalence of AIV among species (Figure 4-4). Prevalence of AIV did not differ (P = 0.130) between 2 species of geese, CAGO and LSGO.

In 2008, we compared 8 species of dabbling ducks: AGWT, AMWI, BWTE, GADW, MALL, NOPI, NSHO, and WODU, and detected differences ($\chi^2 = 163.6$; *P* < 0.001) in prevalence among species (Figure 4-4). Two species of diving ducks, LESC and REDH, and 2 species of geese, CAGO and LSGO, had adequate positive samples for comparison and prevalence of AIV was not different for either group (*P* = 0.557 and *P* = 0.252, respectively).

In 2009, we compared 7 species of dabbling ducks: AGWT, AMWI, BWTE, GADW, MALL, NOPI, and NSHO, and found differences ($\chi^2 = 159.2$; *P* < 0.001) among species (Figure 4-4). The REDH was the only species of diving duck with adequate positive samples so no interspecific comparisons were made. We compared 2 species of geese, CAGO and LSGO, and found prevalence of AIV did not differ between them (*P* = 0.733).

Pacific Flyway. In 2007, we compared 8 species of dabbling ducks: AGWT, AMWI, cinnamon teal ([CITE]; *A. cyanoptera*), GADW, MALL, NOPI, NSHO, and WODU, and found differences ($\chi^2 = 386.2$; *P* < 0.001) in prevalence among species (Figure 4-5). We

compared 2 species of geese and swans, cackling Canada goose ([CACG]; *B. hutchinsii*) and tundra swan ([TUSW]; *C. columbianus*) and found differences (P = 0.007) in prevalence of AIV.

In 2008, we compared 7 species of dabbling ducks: AGWT, AMWI, GADW, MALL, NOPI, NSHO, and WODU, and found differences (P < 0.001) in prevalence existed among species ($\chi^2 = 452.0$; Figure 4-5). We included CACG and LSGO in comparisons from the geese and swans functional group and found differences (P = 0.003) in prevalence of AIV.

In 2009, we compared 7 species of dabbling ducks: AGWT, AMWI, GADW, MALL, NOPI, NSHO, and WODU, and found differences ($\chi^2 = 135.5$; *P* < 0.001) in prevalence among species (Figure 4-5). Only 1 species of diving duck, common goldeneye ([COGO]; *Bucephala clangula*), had adequate positive samples so no comparisons were made. We compared CACG and LSGO from the geese and swans functional group and found no differences (*P* = 0.729) in prevalence between them.

Generalized Linear Mixed Model Analysis

The best-fit model carried 100% of the weight including the parameters: FW, FG, month, year, the interactions of FG and month, FW and month, and FW and year, with the random effect Lat. The second-best model was the global model which carried < 0.001% weight (Table 4-5). The global and null models are included in the table for structural comparison. The calculated AUC for best-fit model was 0.69 (Figure 4-6), indicating an adequate fit to the data. The intercept estimate for the best-fit model represents the Atlantic Flyway, dabbling duck functional group, late October, and 2007. Estimates indicated that prevalence of AIV was higher in the dabbling duck functional

group than all other functional groups. The model also indicated, through the interacton of month and FG, that prevalence of dabbling ducks was higher before late October, but prevalence in diving ducks and geese and swans was higher after late October.

DISCUSSION

The dabbling duck functional group had higher prevalence than any other functional group across all flyways and years according to both our descriptive statistics and mixed model analysis. The HPAIV H5N1 early detection program implemented by the USDA (2006) was designed to target species within the order Anseriformes, thus a high proportion of samples were from dabbling ducks. A suite of factors may influence annual prevalence including: number of juvenile birds, water conditions, food availability, and other environmental conditions that influence stress levels in birds (Munster and Fouchier, 2009). In addition, species-related differences in behavior, spatial and temporal distribution, habitat utilization, migration behavior, population age structure and susceptibility of individual species potentially influence epidemiology of AIV (Stallknecht and Brown, 2007). Prevalence of AIV in dabbling ducks in our study ranged from 9% to 19%. Dabblers from the Atlantic Flyway had 9–12% prevalence with an annual sample size of 6,600–10,400. Surveillance of migratory Eurasian teal (A. crecca), MALL, and NOPI in northern Europe revealed prevalence ranging from 10% to 14% in ~4,300 samples (Wallensten et al., 2007). Munster et al. (2007) sampled ~13,000 dabbling ducks from 9 species including GADW, MALL, NOPI, and NSHO in northern Europe from 1998 to 2006 and reported 6.9% prevalence. Fouchier et al. (2003) reported 2.6% prevalence in ~2,200 wigeon, MALL, NSHO, and teal in northern Europe. Results of surveillance in Europe and the results we report are similar suggesting migratory populations in these areas do not have a large amount of contact with other migratory

birds, so exposure to novel AIVs may be uncommon, thus low prevalences. The Atlantic Flyway had the lowest prevalence of AIV in dabbling ducks in our study.

We suggest the dabbling duck functional group be the emphasis of future AIV surveillance in apparently healthy wild birds because it had highest prevalence yearly. Some species of waterfowl, especially mallards, potentially can be long-distance vectors of HPAIV H5N1 (Keawcharoen et al., 2008). Gaidet et al. (2010) reported that waterfowl may be able to spread HPAIV H5N1 long distances (>350km) during migration periods due to differing asymptomatic infection duration periods in different species, including mallards. In 2010, HPAIV H5N1 was isolated from a healthy mallard (Anas *platyrhynchos*) in South Korea (Kim et al., 2011 *in press*). In 2009, a hunter harvested a mallard positive for HPAIV H5N1, in Germany, with no clinical signs (World Organization for Animal Health, 2009). No mortality was observed in BWTE, MALL, NOPI, and REDH experimentally inoculated with Asian HPAIV H5N1 (Brown et al. 2006). Mallards are abundant across all flyways and were the most collected species during the study. Prevalence of AIV in MALL was >12%. In addition to MALL, NSHO are abundant in all flyways and NOPI are abundant in the western flyways. Prevalence of AIV in NOPI was higher in the Atlantic and Mississippi Flyways and prevalence of AIV in NSHO was higher in the Central and Pacific Flyways. American black ducks are more readily collected in the Atlantic and Mississippi Flyways and had high prevalence, thus continued surveillance for AIV is warranted. American black ducks collected in Ontario had 20% prevalence (Boudreault et al., 1980). The 3 species of teal in our study, AGWT, BWTE, and CITE had high prevalence in all flyways and years. The BWTE is an early migrator and often moves south from breeding grounds in southern Canada and the

Dakotas in late summer arriving at wintering areas on the Gulf Coast of the US in early September (Bellrose, 1976) during the time when prevalence of AIV is thought to be highest in waterfowl. Gadwall, AMWI, and WODU often had lower prevalence than other species of dabbling ducks. Migration timing, food preferences, and habitat selection may decrease contact with infected species or contaminated environments in these species and previous studies confirm our results that these species do not appear to carry AIV as abundantly (Deibel et al., 1985; Ferro et al., 2008; Baumer et al., 2010; Pedersen et al., 2010; Siembieda et al., 2010). Dabbling ducks have high prevalence of many Type A influnezas, so they may be a good surrogate for tracking changes over time in AIVs and for developing risk assessments. We acknowledge, however, that in focusing surveillance efforts for AIV on dabbling ducks we will likely miss some AIVs and these may be of concern. Future AIV surveillance should focus on AGWT, BWTE, MALL, NOPI, and NSHO because these species had the highest prevalence of AIV in the dabbling duck functional group.

Other studies have been conducted on prevalence of AIV in dabbling ducks in North America, South America, and Asia. Prevalence of AIV in mallards in our study was lower (12%-27%) than reported by Parmley et al. (2008). They sampled ducks from 56 locations across Canada and reported 37% (n = 1,572) prevalence of AIV with MALL having highest prevalence (44%). Mallards accounted for 187 of 206 (91%) H5 positive samples. All samples in their study were collected from a single cloacal sample and hatch-year (HY) birds constituted 83% of samples. Samples in our study were collected from both after hatch-year (AHY) and HY birds. The timing and age structure of the samples collected by Parmley et al. (2008) likely led to the higher prevalences than we report. Ducks were sampled for AIV in coastal Louisiana in 1986–1987 (Stallknecht et al., 1990). Cloacal and tracheal swabs were collected from 1,389 ducks during September–January and prevalence decreased from 3.1% to 0.4% over the period. Bluewinged teal constituted 20% of all birds sampled. Prevalence of AIV in BWTE in the Mississippi Flyway in our study ranged from 11% to 17%, but prevelance declines on wintering grounds (Halvorson et al., 1985; Munster et al., 2007; Wallensten et al., 2007). We found higher prevalence of AIV in dabbling ducks (13%-16%) and diving ducks (4%-7%) in the Central Flyway, and NOPI (15%-18%), but prevalences for MALL (14%-18%) and BWTE (20%-22%) were similar to those of Ferro et al. (2008), Hanson et al. (2005), and Hanson et al. (2003). In Minnesota, cloacal swabs were collected from MALL and NOPI and prevalence of AIV was 18% in MALL and 2.9% in NOPI (Hanson et al., 2003). Ten H5 positive samples in that study were collected (0.7%) and 60% of sampled birds were HY. Wintering waterfowl, including AGWT, AMWI, BWTE, GADW, MODU, and NSHO, were collected for surveillance of AIV from the Gulf Coast of Texas (Ferro et al., 2008). Prevalence was 5.9% in dabbling ducks and 2% in diving ducks. Along the Gulf Coast of Texas, cloacal swabs were collected from 258 live ducks with BWTE making up 42% of the sample and MODU making up 35% of the sample (Hanson et al., 2005). Prevalence ranged from 0% to 15% over the study period. The H5 subtype was not detected in any samples. Our results were in the range of those prevalences previously reported.

The diving duck and geese and swans functional groups had significantly (P < 0.05) lower prevalence than the dabbling ducks across our entire study. Differences in feeding habits likely caused the difference in prevalence. Diving ducks use deeper water

areas than dabbling ducks and geese and swans often graze on terrestrial vegetation or waste grain and are not as routinely subjected to the shallow water feeding areas that are thought to transmit AIV to dabbling ducks (Bellrose, 1976; Takekawa et al., 2010). Geese and swans are equally susceptible to AIV as dabbling ducks but feeding habits may lead to less efficient transmission (Wahlgren, 2011). Some overlap in habitat necessarily occurs, especially during migrations, thus transmission of AIV due to contaminated environments. Sampling of diving ducks should occur after late October as indicated by our model. Outbreaks of HPAIV H5N1 in Europe have occurred in a limited number of species including mute swans, whooper swans (C. cygnus), CAGO, and tufted ducks ([A. fuligula]; Sabirovic et al., 2006; Teifke et al., 2007) in addition to a clinically healthy common pochard (A. ferina) in Switzerland and MUSW in Germany (Baumer et al., 2010; Breed et al., 2010), so continued surveillance for AIV in diving ducks and geese and swans in North America is warranted. Delayed illness and death of experimentally infected whooper, mute, and trumpeter (*C. buccinator*) swans indicates these species may actively shed virus during migratory movements (Brown et al., 2008) and may be a link in long-distance spread of AIV. Conversely, van Gils et al. (2007) found that Bewick's swans (C. columbinaus) infected with LPAIV experienced delayed migration, shorter movements and reduced feeding rates. Prevalence in geese and swans in the Atlantic Flyway during our study was 2%–4% with ~17,000 samples collected. Six species of geese and 2 species of swans were collected in northern Europe from 1998 to 2006 for surveillance of AIV with reported prevalence of 1.7% in 6,628 samples collected (Munster et al., 2007). In addition, Fouchier et al., (2003) reported 1.4% prevalence of AIV in 1,387 GWFG, graylag geese (A. anser), and brent geese (B.

bernicla). Prevalence of AIV in geese and swans in the Pacific Flyway was 4%-6% in samples collected during our surveillance. Whistling swans (*C. columbianus*) and GWFG (n = 1,022) were collected in HPAIV H5N1 endemic areas of Japan in 1997–2000 (Shengqing et al., 2002). The birds had 1.9% prevalence with no H5 or H7 subtypes discovered. Canada geese on 8 national refuges in all flyways except the Pacific were tested for AIV (Winkler et al., 1972). Prevalence was 4.7% in 1,401 birds and the authors concluded that resident non-migratory flocks had higher prevalence than migratory flocks. We suggest surveillance for AIV in resident flocks of CAGO should be conducted during periods when mixing with migratory waterfowl could occur. Sampling of migratory geese and swans should occur concurrently with diving ducks during the fall migration period after late October as indicated by our model.

Shorebirds and gulls and terns had significantly lower prevalence of AIV than dabbling ducks in our study. The Atlantic Flyway was the main focus of shorebird and gull and tern collection due to possible overlapping migratory patterns with European flyways and potential to meet minimum sample reqirements (DeLiberto et al., 2011 *in press*). Many shorebird species in the Northern Hemisphere are long distance intercontinental migrants and may have potential to distribute AIV around the globe (van de Kam et al., 2004; Olsen et al., 2006). Seasonal peaks of AIV in shorebirds were in the spring (Kawaoka et al., 1988; Krauss et al., 2004; Hanson et al., 2008), unlike ducks that experience peaks in the late summer. Shorebirds may carry LPAIV north in the spring to breeding areas (Krauss et al., 2004). Shorebirds, gulls and terns were sampled in Argentina, Bermuda, Chile, Texas, and in the Atlantic, Mississippi, and Central Flyways from September, 1999 to November, 2005 (Hanson et al., 2008). No positive samples were collected outside the US (n = 707). Avian influenza virus was discovered in 2 RBGU in 2000 and 2001and 1 REKN in 2001 from Georgia but overall prevalence was low (2%, 3%, and 1%, respectively). In addition, 3 LAGU (1%) and 1 HERG (6%) collected in New York in 2000 were positive for AIV and a single positive LESA (3%) was collected in Texas. Hanson et al. (2008) reported prevalence of AIV was higher in birds migrating through the Delaware Bay than all other sites (4.4% and 0.3%, respectively).

Shorebird and gull and tern sample sizes in our study ranged from 1,000 to 5,000 yearly. Prevalence of AIV in shorebirds was steady at $\sim 7\%$ in 2007–2009. Shorebirds use shallow water habitats for feeding, leading to overlap with dabbling ducks, which can lead to AIV exposure. In Asia, gulls have been infected with HPAIV H5N1 in the presence of other infected waterfowl (Chen et al., 2005) but generally, dabbling ducks and gulls and terns do not have overlapping habitats and due to their ecology, gulls infected with HPAIV H5N1 likely were scavenging remains of dead waterfowl (Barnard and Thompson, 1985). Avian influenza virus subtypes H9 and H13 are most commonly isolated in shorebirds and gulls (Kawaoka et al., 1988; Graves, 1992). Subtype H9 rarely is reported in ducks and geese, and H13 is exclusive to shorebirds and gulls (Alexander, 2000; Fouchier et al., 2005). Experimental infection of ducks with AIV isolated from shorebirds and gulls failed, suggesting host adaptation (Hinshaw et al., 1982; Kawaoka et al., 1988). Results of surveillance for AIV in northern Europe were similar to our findings that gulls had low prevalence of AIV (0.8% and 1.1%; Munster et al., 2007 and Fouchier et al., 2003, respectively). We suggest sampling for AIV in shorebirds in the fall where habitat overlap with dabbling ducks is likely.

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Year	Functional Group	Prevalence (%)	95% CI	n
2007	Dabbling Ducks	9.29	8.73–9.86	10,359
	Diving Ducks	3.07	2.42-3.83	2,413
	Geese and Swans	3.65	3.09-4.29	3,942
	Gulls and Terns	4.63	3.61–5.84	1,468
	Shorebirds	5.56	4.53-6.73	1,764
2008	Dabbling Ducks	11.93	11.30–12.58	10,011
	Diving Ducks	4.67	3.93-5.50	2,934
	Geese and Swans	3.80	3.28-4.38	4,836
	Gulls and Terns	7.28	5.28-8.96	1,113
	Shorebirds	6.46	5.15–7.99	1,223
2009	Dabbling Ducks	11.40	10.64–12.19	6,580
	Diving Ducks	4.86	3.97–5.89	2,035
	Geese and Swans	2.29	1.75–2.84	2,877
	Shorebirds	6.29	4.88–7.94	1,034

Table 4-1. Prevalence of avian influenza virus by functional group in the Atlantic Flyway, US, 2007–2009.

Year	Functional Group	Prevalence (%)	95% CI	п
2007	Dabbling Ducks	11.11	10.56–11.68	12,245
	Diving Ducks	3.85	2.78-5.19	1,064
	Geese and Swans	1.60	1.08–2.30	1,808
2008	Dabbling Ducks	13.80	13.20–14.41	12,624
	Diving Ducks	6.63	5.24-8.25	1,116
	Geese and Swans	2.18	1.67–2.80	2,748
	Gulls and Terns	5.47	2.76–9.58	201
2009	Dabbling Ducks	19.41	18.61–20.23	9,309
	Diving Ducks	11.11	9.05–13.45	828
	Geese and Swans	2.42	1.70–3.34	1,486

Table 4-2. Prevalence of avian influenza virus by functional group in the Mississippi Flyway, US, 2007–2009.

Year	Functional Group	Prevalence (%)	95% CI	n
2007	Dabbling Ducks	13.20	12.54–13.87	9,860
	Diving Ducks	3.55	2.37-5.09	789
	Geese and Swans	2.83	2.00-3.88	1,307
2008	Dabbling Ducks	13.85	13.18–14.53	10,292
	Diving Ducks	6.54	4.92-8.49	795
	Geese and Swans	5.65	4.72–6.71	2,158
2009	Dabbling Ducks	15.65	14.87–16.44	8,379
	Diving Ducks	6.68	4.72–9.13	539
	Geese and Swans	5.97	4.66–7.52	1,122

Table 4-3. Prevalence of avian influenza virus by functional group in the Central Flyway, US, 2007–2009.

Year	Functional Group	Prevalence (%)	95% CI	n
2007	Dabbling Ducks	16.12	15.39–16.87	9,602
	Diving Ducks	3.55	2.18-5.42	564
	Geese and Swans	5.28	4.27-6.45	1,705
2008	Dabbling Ducks	15.59	14.88–16.31	9,976
	Diving Ducks	6.65	4.56–9.31	466
	Geese and Swans	4.40	3.42-5.52	1,612
2009	Dabbling Ducks	14.53	13.37–15.36	7,273
	Diving Ducks	7.90	5.08-11.62	291
	Geese and Swans	5.68	4.35–7.27	1,038

Table 4-4. Prevalence of avian influenza virus by functional group in the Pacific Flyway, US, 2007–2009.

Table 4-5. The best-fit, global, and null models from the generalized linear mixed model analysis of avian influenza virus infection in samples collected from migratory birds in the US, 2007–2009.

Model	Explanatory variables	k	BIC	Δ BIC	weight	AUC
Best-fit	FW + FG + Month + Year +	36	104,379	0	1	0.69
	FW*Month + FG*Month +					
	Year*FW + Lat					
Global	FW + FG + Month + Year +	46	104,430	51	< 0.001	-
	FW*Month + FG*Month +					
	Year*FW + FG*Year + Lat					
Null	1 + Year + Lat	4	110,544	6,161	0	-

PN = positive/negative avian influenza infection, FW = flyway (Atlantic, Mississippi, Central, Pacific), FG = functional group (dabbling duck, diving duck, geese and swan, shorebird, gull and tern, other water bird), Lat = latitude (24°–68° N), * = interaction of 2 parameters, BIC = Bayesian Information Criterion, AUC = area under the receiver operating curve predicting the fit of the model

Table 4-6. Estimates and *P* values from the generalized linear mixed model PN ~ FW + FG + Month + Year + FW*Month + FG*Month + Year*FW + Lat, predicting avian influenza virus infection in migratory birds in the US, 2007–2009.

Coefficient	Estimate	SE	z value	<i>P</i> (> z)
Intercept ¹	-2.6373	0.1349	-19.549	< 0.0001
FWC	0.0853	0.0464	1.837	0.0662
FWM	0.1504	0.0447	3.362	0.0008
FWP	0.5220	0.0456	11.469	< 0.0001
FGdiv	-1.0930	0.0511	-21.396	< 0.0001
FGgs	-1.6924	0.0518	-26.415	< 0.0001
FGgt	-0.6146	0.1019	-6.031	< 0.0001
FGo	-1.5308	0.2751	-5.564	< 0.0001
FGsb	-2.6684	0.1744	-15.302	< 0.0001
Month	-0.1794	0.0221	-8.110	< 0.0001
Year2008	0.2692	0.0391	6.880	< 0.0001
Year2009	0.3227	0.0452	7.143	< 0.0001
FWC*Month	-0.3342	0.0332	-10.072	< 0.0001
FWM*Month	0.1550	0.0302	5.130	< 0.0001
FWP*Month	-0.3725	0.0332	-11.232	< 0.0001
FGdiv*Month	0.4710	0.0635	7.417	< 0.0001
FGgs*Month	0.6055	0.0331	18.309	< 0.0001
FGgt*Month	-0.4341	0.1168	-3.717	0.0002

Coefficient	Estimate	SE	z value	P (> z)
FGo*Month	1.1912	0.3815	3.122	0.0018
FGsb*Month	-0.3587	0.1941	-1.848	0.0646
FWC*2008	-0.0834	0.0564	-1.480	0.1388
FWM*2008	0.0242	0.0544	0.444	0.6569
FWP*2008	-0.2676	0.0552	-4.850	< 0.0001
FWC*2009	-0.0114	0.0620	-0.184	0.8543
FWM*2009	0.2737	0.0593	4.613	< 0.0001
FWP*2009	-0.3726	0.0625	-5.959	< 0.0001

PN = positive/negative avian influenza infection, FW = flyway (C = Central, M =

Mississippi, P = Pacific), FG = functional group (div = diving ducks, gs = geese and swans, gt = gulls and terns, o = other water birds, sb = shorebirds), Lat = latitude, * = interaction of 2 parameters

¹ The intercept included the parameters for the Atlantic Flyway, dabbling duck functional group, late October, and 2007.



Figure 4-1. Major migratory bird flyways in the US (Lincoln, 1935).



Figure 4-2. Prevalence of avian influenza virus in dabbling ducks from the Atlantic Flyway, 2007–2009 (n = 23,827).

ABDU = American black duck, AGWT = American green-winged teal, AMWI = American wigeon, BWTE = Blue-winged teal, MALL = Mallard, MODU = Mottled duck, NOPI = Northern pintail, NSHO = Northern shoveler, WODU = Wood duck



Figure 4-3. Prevalence of avian influenza virus in dabbling ducks from the Mississippi Flyway, 2007–2009 (n = 34,178).

ABDU = American black duck, AGWT = American green-winged teal, AMWI = American wigeon, BWTE = Blue-winged teal, GADW = Gadwall, MALL = Mallard, NOPI = Northern pintail, NSHO = Northern shoveler, WODU = Wood duck



Figure 4-4. Prevalence of avian influenza virus in dabbling ducks from the Central Flyway, 2007–2009 (n = 28,531).

AGWT = American green-winged teal, AMWI = American wigeon, BWTE = Bluewinged teal, GADW = Gadwall, MALL = Mallard, NOPI = Northern pintail, NSHO = Northern shoveler, WODU = Wood duck



Figure 4-5. Prevalence of avian influenza virus in dabbling ducks from the Pacific Flyway, 2007–2009 (n = 26,851).

AGWT = American green-winged teal, AMWI = American wigeon, GADW = Gadwall, MALL = Mallard, NOPI = Northern pintail, NSHO = Northern shoveler, WODU = Wood duck



Figure 4-6. The area under the curve (AUC) of the receiver operating curve (ROC) predicting the fit of the model: PN ~ FW + FG + Month + Year + FW*Month + FG*Month + Year*FW + Lat, that addresses the prevalence of avian influenza virus in sampled birds in the US, 2007–2009.

PN = positive/negative avian influenza infection, FW = flyway, FG = functional group, Lat = latitude, * = interaction of 2 parameters.

- 1) $PN \sim 1 + Year + Lat$
- 2) $PN \sim FW + Year + Lat$
- 3) $PN \sim FG + Year + Lat$
- 4) $PN \sim FW + FG + Year + Lat$
- 5) $PN \sim Month + Year + Lat$
- 6) $PN \sim FW + Month + Year + Lat$
- 7) $PN \sim FG + Month + Year + Lat$
- 8) $PN \sim FW + FG + Month + Year + Lat$
- 9) $PN \sim FW + Month + Year + Year*FW + Lat$
- 10) $PN \sim FW + FG + Month + Year + Year*FW + Lat$
- 11) $PN \sim FG + Month + Year + FG*Month + Lat$
- 12) $PN \sim FW + FG + Month + Year + FG*Month + Lat$
- 13) $PN \sim FW + FG + Year + FG*FW + Lat$
- 14) $PN \sim FW + FG + (Month + Year + FG*FW + Lat)$
- 15) $PN \sim FW + Month + Year + FW*Month + Lat$
- 16) $PN \sim FW + FG + Month + Year + FW*Month + Lat$
- 17) $PN \sim FW + FG + Month + fYear + FW*Month + FG*Month + Lat$
- 18) $PN \sim FW + Month + Year + FW*Month + Year*FW + Lat$
- 19) $PN \sim FW + FG + Month + Year + FW*Month + Year*FW + Lat$
- 20) PN ~ FW + FG + Month + Year + FW*Month + FG*Month + Year*FW + Lat

- 21) $PN \sim FW + FG + Year + FG^*Year + Lat$
- 22) $PN \sim FG + Month + Year + FG*Year + Lat$
- 23) $PN \sim FW + FG + Month + Year + FG*Year + Lat$
- 24) $PN \sim FW + FG + Year + Year*FW + FG*Year + Lat$
- 25) $PN \sim FW + FG + Month + Year + Year*FW + FG*Year + Lat$
- 26) $PN \sim FG + Month + Year + FG*Month + FG*Year + Lat$
- 27) $PN \sim FW + FG + Month + Year + FG*Month + FG*Year + Lat$
- 28) $PN \sim FW + FG + Month + Year + FG^*FW + FG^*Year + Lat$
- 29) PN ~ FW + FG + Month + Year + FW*Month + FG*Year + Lat
- 30) PN ~ FW + FG + Month + Year + FW*Month + FG*Month + FG*Year + Lat
- 31) PN ~ FW + FG + Month + Year + FW*Month + Year*FW + FG*Year + Lat
- 32) PN ~ FW + FG + Month + Year + FW*Month + FG*Month + Year*FW +

FG*Year + Lat

PN = positive/negative avian influenza infection, FW = flyway, FG = functional group, Lat = lat, * = interaction of 2 parameters.

Appendix C. Summary of number of positive avian influenza virus samples and the total sample size by year, flyway, and species within the dabbling duck functional group in the US, 2007–2009.

Year	Flyway	Species	Positive / Total Sample	%
2007	Atlantic	American black duck	116/975	11.9
		American green-winged teal	184/1,989	9.3
		Blue-winged teal	20/420	4.8
		Gadwall	11/373	3.0
		Mallard	490/3,377	14.5
		Mottled duck	18/214	8.4
		Northern pintail	37/289	12.8
		Northern shoveler	11/347	3.6
		Wood duck	33/1,658	2.0
2007	Mississippi	American black duck	32/138	23.2
		American green-winged teal	204/1,601	12.7
		American wigeon	29/366	7.9
		Blue-winged teal	172/1,355	12.7
		Gadwall	35/1,173	3.0
		Mallard	523/4,473	11.7
		Northern pintail	189/1,025	18.4
		Northern shoveler	128/879	14.6
		Wood duck	47/1,216	3.9
2007	Central	American green-winged teal	132/1,196	11.0

Year	Flyway	Species	Positive / Total Sample	%
2007	Central	American wigeon	27/725	3.7
		Blue-winged teal	326/1,673	19.5
		Gadwall	35/840	4.2
		Mallard	514/3,632	14.2
		Northern pintail	185/1,032	17.9
		Northern shoveler	51/545	9.4
		Wood duck	27/128	21.1
2007	Pacific	American green-winged teal	198/1,389	14.3
		American wigeon	64/1,105	5.8
		Cinnamon teal	10/87	11.5
		Gadwall	42/548	7.7
		Mallard	887/3,606	24.6
		Northern pintail	156/1,424	11.0
		Northern Shoveler	174/1,014	17.2
		Wood duck	10/352	2.8
2008	Atlantic	American black duck	92/857	10.7
		American green-winged teal	256/1,924	13.3
		American wigeon	13/342	3.8
		Blue-winged teal	36/396	9.1
		Mallard	681/3,359	20.3
		Mottled duck	20/256	7.8
		Northern pintail	25/237	10.6

Year	Flyway	Species	Positive / Total Sample	%
2008	Atlantic	Northern shoveler	19/261	7.3
		Wood duck	40/1,858	2.2
2008	Mississippi	American black duck	35/172	20.4
		American green-winged teal	305/2,235	13.7
		American wigeon	77/490	15.7
		Blue-winged teal	154/1,406	11.0
		Gadwall	53/1,072	5.0
		Mallard	754/4,564	16.5
		Mottled duck	18/211	8.5
		Northern pintail	175/810	21.6
		Northern shoveler	115/661	17.4
		Wood duck	55/937	5.5
2008	Central	American green-winged teal	195/1,503	13.0
		American wigeon	44/689	6.4
		Blue-winged teal	325/1,560	20.8
		Gadwall	38/772	4.7
		Mallard	537/3,370	13.7
		Northern pintail	169/1,064	15.9
		Northern shoveler	52/365	14.3
		Wood duck	61/326	18.7
2008	Pacific	American green-winged teal	181/1,549	11.7
		American wigeon	57/1,208	4.7

Year	Flyway	Species	Positive / Total Sample	%
2008	Pacific	Gadwall	29/594	4.9
		Mallard	923/3,743	24.7
		Northern pintail	142/1,439	9.9
		Northern shoveler	153/940	16.3
		Wood duck	49/354	13.8
2009	Atlantic	American black duck	181/714	25.4
		American green-winged teal	145/1,428	10.2
		American wigeon	14/241	5.8
		Blue-winged teal	44/531	8.3
		Mallard	266/1,745	15.2
		Mallard-black duck hybrid	19/89	21.4
		Mottled duck	22/295	7.5
		Northern pintail	16/163	9.8
		Northern shoveler	19/239	8.0
2009	Mississippi	American black duck	30/97	30.1
		American green-winged teal	305/1,402	21.8
		American wigeon	38/230	16.5
		Black-bellied whistling duck	12/52	18.8
		Blue-winged teal	250/1,475	17.0
		Gadwall	83/593	12.3
		Mallard	729/2,704	27.0
		Northern pintail	207/758	27.3

Year	Flyway	Species	Positive / Total Sample	%
2009	Mississippi	Northern shoveler	106/493	21.5
		Wood duck	46/1,191	3.9
2009	Central	American green-winged teal	115/904	12.7
		American wigeon	27/607	4.5
		Blue-winged teal	283/1,277	22.2
		Gadwall	43/650	6.6
		Mallard	642/3,653	17.6
		Northern pintail	133/904	14.7
		Northern shoveler	52/258	20.2
2009	Pacific	American green-winged teal	158/1,375	11.5
		American wigeon	96/796	12.1
		Gadwall	21/346	6.1
		Mallard	468/2,225	21.0
		Northern pintail	182/1,523	12.0
		Northern shoveler	109/663	16.4
		Wood duck	11/221	5.0

Appendix D. Summary of number of positive avian influenza virus samples and the total sample size by year, flyway, and species within the diving duck functional group in the US, 2007–2009.

Year	Flyway	Species	Positive / Total Sample	%
2007	Atlantic	Bufflehead	11/434	2.5
		Canvasback	10/150	6.7
		Lesser scaup	12/223	5.4
		Ring-necked duck	13/624	2.1
2008	Atlantic	Bufflehead	41/783	5.2
		Lesser scaup	21/407	5.2
		Ring-necked duck	30/570	5.3
		Ruddy duck	15/141	10.6
2008	Mississippi	Lesser scaup	17/300	5.7
		Redhead	10/51	19.6
		Ring-necked duck	30/404	7.4
2008	Central	Lesser scaup	11/130	8.5
		Redhead	24/348	6.9
2009	Atlantic	Bufflehead	51/757	6.7
		Ring-necked duck	21/422	5.0
2009	Mississippi	Bufflehead	16/87	22.5
		Lesser scaup	28/131	21.4
		Redhead	12/142	8.5
		Ring-necked duck	25/298	8.4

Year	Flyway	Species	Positive / Total Sample	%
2009	Central	Redhead	22/255	8.6
	Pacific	Common Goldeneye	10/54	18.5

Appendix E. Summary of number of positive avian influenza virus samples and the total sample size by year, flyway, and species within the geese and swans functional group in the US, 2007–2009.

Year	Flyway	Species	Positive / Total Sample	%
2007	Atlantic	Canada goose	99/3,000	3.3
		Greater snow goose	39/228	17.1
2007	Central	Canada goose	23/848	2.7
		Lesser snow goose	11/225	4.9
2007	Pacific	Cackling Canada goose	47/333	14.1
		Tundra swan	22/303	7.3
2008	Atlantic	Canada goose	52/3,365	1.6
		Greater snow goose	102/469	21.8
		Mute swan	14/263	5.3
2008	Mississippi	Canada goose	19/1,834	1.0
		Lesser snow goose	27/314	8.6
2008	Central	Canada goose	76/1,418	5.4
		Lesser snow goose	32/470	6.8
2008	Pacific	Cackling Canada goose	37/337	11.0
		Lesser snow goose	10/230	4.2
2009	Atlantic	Atlantic brant	21/348	6.0
		Canada goose	16/1,870	0.9
		Greater snow goose	26/494	5.3
2009	Mississippi	Canada goose	20/857	2.3

Year	Flyway	Species	Positive / Total Sample	%
2009	Central	Canada goose	45/725	6.2
2009	Pacific	Lesser snow goose	10/193	5.2
		Cackling Canada goose	14/102	13.7
		Lesser snow goose	35/286	12.2

Appendix F. Summary of number of positive avian influenza virus samples and the total sample size by year, flyway, and species within the gulls and terns functional group in the US, 2007–2009.

Year	Flyway	Species	Positive / Total Sample	%
2007	Atlantic	Common tern	11/218	5.1
		Herring gull	29/505	5.7
		Ring-billed gull	24/537	4.5
2008	Atlantic	Herring gull	26/562	4.6
		Ring-billed gull	53/245	21.6
Appendix G. Summary of number of positive avian influenza virus samples and the total sample size by flyway, year, and species within the shorebirds functional group in the US, 2007–2009.

Year	Flyway	Species	Positive / Total Sample	%
2007	Atlantic	Red knot	13/282	4.6
		Ruddy turnstone	26/199	13.1
		Semipalmated sandpiper	36/338	9.6
		Western sandpiper	12/33	36.4

Flyway	Year	Species	ABDU	AGWT	BWTE	GADW	MALL	MODU	NOPI	NSHO
Atlantic	2007	AGWT	0.028							
		BWTE	< 0.001	0.002						
		GADW	< 0.001	< 0.001	0.024					
		MALL	0.041	< 0.001	< 0.001	< 0.001				
		MODU	0.154	0.803	0.077	0.005	0.011			
		NOPI	0.682	0.070	0.002	< 0.001	0.485	0.142		
		NSHO	< 0.001	< 0.001	0.357	1.000	< 0.001	0.010	< 0.001	
		WODU	< 0.001	< 0.001	0.003	0.241	< 0.001	< 0.001	< 0.001	0.223
			ABDU	AGWT	AMWI	BWTE	MALL	MODU	NOPI	NSHO
Atlantic	2008	AGWT	0.063							
		AMWI	< 0.001	< 0.001						
		BWTE	0.422	0.020	0.005					
		MALL	< 0.001	< 0.001	< 0.001	< 0.001				

Appendix H. Species to species comparisons (P) of prevalence of avian influenza virus in dabbling ducks, US flyways, 2007–2009.

Flyway	Year	Species	ABDU	AGWT	AMWI	BWTE	MALL	MODU	NOPI	NSHO
Atlantic	2008	MODU	0.194	0.012	0.045	0.668	< 0.001			
		NOPI	1.000	0.261	0.002	0.579	0.001	0.348		
		NSHO	0.124	0.005	0.068	0.473	< 0.001	0.869	0.210	
		WODU	< 0.001	< 0.001	0.082	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
			ABDU	AGWT	AMWI	BWTE	MALL	MBDH	MODU	NOPI
Atlantic	2009	AGWT	< 0.001							
		AMWI	< 0.001	0.033						
		BWTE	< 0.001	0.229	0.243					
		MALL	< 0.001	< 0.001	< 0.001	< 0.001				
		MBDH	0.439	0.002	0.001	0.001	0.133			
		MODU	< 0.001	0.162	0.492	0.789	< 0.001	0.001		
		NOPI	< 0.001	1.000	0.175	0.527	0.065	0.014	0.382	
		NSHO	< 0.001	0.348	0.373	1.000	0.002	0.002	0.871	0.590

Flyway	Year	Species	ABDU	AGWT	AMWI	BWTE	GADW	MALL	NOPI	NSHO	
Mississippi	2007	AGWT	0.002								
		AMWI	< 0.001	0.009							
		BWTE	0.002	1.000	0.010						
		GADW	< 0.001	< 0.001	0.001	< 0.001					
		MALL	0.002	0.282	0.032	0.315	< 0.001				
		NOPI	0.203	< 0.001	< 0.001	0.001	< 0.001	< 0.001			
		NSHO	0.012	0.218	0.001	0.228	< 0.001	0.021	0.026		
		WODU	< 0.001	< 0.001	0.003	< 0.001	0.262	< 0.001	< 0.0001	< 0.001	
			ABDU	AGWT	AMWI	BWTE	GADW	MALL	MODU	NOPI	NSHO
Mississippi	2008	AGWT	0.022								
		AMWI	0.193	0.250							
		BWTE	< 0.001	0.018	0.006						
		GADW	< 0.001	< 0.001	< 0.001	< 0.001					
		MALL	0.210	0.002	0.700	< 0.001	< 0.001				

Flyway	Year	Species	ABDU	AGWT	AMWI	BWTE	GADW	MALL	MODU	NOPI	NSHO
Mississippi	2008	MODU	0.001	0.034	0.011	0.338	0.047	0.002			
		NOPI	0.760	< 0.001	0.009	< 0.001	< 0.001	0.006	< 0.001		
		NSHO	0.374	0.020	0.472	< 0.001	< 0.001	0.576	0.001	0.048	
		WODU	< 0.001	< 0.001	< 0.001	< 0.001	0.554	< 0.001	0.112	< 0.001	< 0.001
			ABDU	AGWT	AMWI	BBWD	BWTE	GADW	MALL	NOPI	NSHO
Mississippi	2009	AGWT	0.043								
		AMWI	0.005	0.081							
		BBWD	0.100	0.644	0.708						
		BWTE	0.001	0.001	0.925	0.734					
		GADW	< 0.001	< 0.001	0.116	0.168	0.006				
		MALL	0.416	< 0.001	< 0.001	0.155	< 0.001	< 0.001			
		NOPI	0.471	0.004	< 0.001	0.184	< 0.001	< 0.001	0.853		
		NSHO	0.048	0.949	0.134	0.745	0.026	< 0.001	0.012	0.023	
		WODU	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001

Flyway	Year	Species	AGWT	AMWI	BWTE	GADW	MALL	NOPI	NSHO
Central	2007	AMWI	< 0.001						
		BWTE	< 0.001	< 0.001					
		GADW	< 0.001	0.698	< 0.001				
		MALL	0.006	< 0.001	< 0.001	< 0.001			
		NOPI	< 0.001	< 0.001	0.390	< 0.001	0.002		
		NSHO	0.313	< 0.001	< 0.001	< 0.001	0.003	< 0.001	
		WODU	0.002	< 0.001	0.645	< 0.001	0.039	0.400	< 0.001
			AGWT	AMWI	BWTE	GADW	MALL	NOPI	NSHO
Central	2008	AMWI	< 0.001						
		BWTE	< 0.001	< 0.001					
		GADW	< 0.001	0.172	< 0.001				
		MALL	0.478	< 0.001	< 0.001	< 0.001			
		NOPI	0.039	< 0.001	0.002	< 0.001	0.083		
		NSHO	0.547	< 0.001	0.004	< 0.001	0.812	0.502	

Flyway	Year	Species	AGWT	AMWI	BWTE	GADW	MALL	NOPI	NSHO
Central	2008	WODU	0.008	< 0.001	0.407	< 0.001	0.016	0.234	0.123
			AGWT	AMWI	BWTE	GADW	MALL	NOPI	
Central	2009	AMWI	< 0.001						
		BWTE	< 0.001	< 0.001					
		GADW	< 0.001	0.110	< 0.001				
		MALL	< 0.001	< 0.001	< 0.001	< 0.001			
		NOPI	0.245	< 0.001	< 0.001	< 0.001	0.043		
		NSHO	0.004	< 0.001	0.509	< 0.001	0.311	0.042	
			AGWT	AMWI	BWTE	GADW	MALL	NOPI	NSHO
Pacific	2007	AMWI	< 0.001						
		BWTE	0.529	0.059					
		GADW	< 0.001	0.165	0.212				
		MALL	< 0.001	< 0.001	0.003	< 0.001			
		NOPI	0.009	< 0.001	0.860	0.030	< 0.001		

Flyway	Year	Species	AGWT	AMWI	BWTE	GADW	MALL	NOPI	NSHO
Pacific	2007	NSHO	0.060	< 0.001	0.230	< 0.001	< 0.001	< 0.001	
		WODU	< 0.001	0.026	0.002	0.002	< 0.001	< 0.001	< 0.001
			AGWT	AMWI	GADW	MALL	NOPI	NSHO	
Pacific	2008	AMWI	< 0.001						
		GADW	< 0.001	0.907					
		MALL	< 0.001	< 0.001	< 0.001				
		NOPI	0.112	< 0.001	< 0.001	< 0.001			
		NSHO	0.001	< 0.001	< 0.001	< 0.001	< 0.001		
		WODU	0.278	< 0.001	< 0.001	< 0.001	0.034	0.303	
			AGWT	AMWI	GADW	MALL	NOPI	NSHO	
Pacific	2009	AMWI	0.729						
		GADW	0.003	0.002					
		MALL	< 0.001	< 0.001	< 0.001				
		NOPI	0.729	0.946	0.001	< 0.001			

Flyway	Year	Species	AGWT	AMWI	GADW	MALL	NOPI	NSHO
Pacific	2009	NSHO	0.003	0.019	< 0.001	0.009	0.005	
		WODU	0.002	0.002	0.710	< 0.001	0.001	< 0.001

ABDU = American black duck, AGWT = American green-winged teal, AMWI = American wigeon, BBWD = Black-bellied whistling duck, BWTE = Blue-winged teal, GADW = Gadwall, MALL = Mallard, MBDH = Mallard/black duck hybrid, MODU = Mottled Duck, NOPI = Northern pintail, NSHO = Northern shoveler, WODU = Wood duck

Fisher's Exact Tests were performed for comparisons (Fisher, 1925).

Appendix I. Species to species comparisons (*P*) of prevalence of avian influenza virus in diving ducks in U.S flyways, 2007–2009.

Flyway	Year	Species	BUFF	CANV	LESC
Atlantic	2007	CANV	0.022		
		LESC	0.070	0.657	
		RNDU	0.681	0.998	0.019
			BUFF	LESC	REDH
Mississippi	2009	LESC	0.860		
		REDH	0.009	0.003	
		RNDU	0.003	< 0.001	1.000

CANV = Canvasback, LESC = Lesser scaup, REDH = Redhead, RNDU = Ring-necked

duck, RUDU = Ruddy duck

Fisher's Exact Tests were performed for comparisons (Fisher, 1925).

Appendix J. Species to species comparisons (*P*) of prevalence of avian influenza virus in geese and swans in U.S flyways, 2007–2009.

Flyway	Year	Species	CAGO	GSGO
Atlantic	2008	GSGO	< 0.001	
		MUSW	< 0.001	< 0.001
			ATBR	CAGO
Atlantic	2009	CAGO	< 0.001	
		GSGO	0.650	< 0.001

ATBR = Atlantic brant, CAGO = Canada goose, GSGO = Greater snow goose, MUSW =

Mute swan

Fisher's Exact Tests were performed for comparisons (Fisher, 1925).

CHAPTER 5: EFFECTS OF SEPTEMBER HUNTING SEASONS ON SURVIVAL, HARVEST, AND RECOVERY RATES OF CANADA GEESE BANDED IN SOUTHEAST NEBRASKA

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Abstract: Restoration efforts in Nebraska have contributed to increased populations of resident Canada geese (*Branta canadensis*). Populations have grown to levels that now are considered a nuisance and damage has exceeded public tolerance. An early September hunting season was initiated in southeast Nebraska in 2004 to reduce populations of resident Canada geese. We analyzed band returns from Canada geese banded in southeast Nebraska to determine if early hunting seasons affected survival, harvest, and recovery rates. Our survival analysis revealed that early seasons did not reduce survival of geese (*S* [AHY] = 0.696, 95% C.I. = 0.679–0.713, *S*' [HY] = 0.896, 95% C.I. = 0.786–0.953). In addition, the top model estimated a combined survival for geese inside and outside the early hunting zone (southeast versus northeast Nebraska, *S* = 0.711, 95% C.I. = 0.666–0.752) and survival did not differ by sex (*S* = 0.630–0.816) but it varied yearly. We detected differences in survival between the metropolitan areas of Omaha (*S* = 0.742, 95% C.I. = 0.688–0.790) and Lincoln, Nebraska, (0.678, 95% C.I. = 0.651–0.703). Seventy-three percent of all recoveries of geese banded after hatch-year

and 71% of all recoveries of geese banded hatch-year were from Nebraska. September hunting seasons affected timing of recovery as 23%–49% of annual band recoveries for the hunting season occurred during the month of September. Prior to the establishment of early September hunting seasons, November was the month with the highest number of recoveries of both AHY and HY geese (27% and 38%, respectively). A high degree of urbanization in this region of the state may be leading to higher survival and control methods other than hunting should be explored to reduce populations.

Key words: band analysis, *Branta canadensis*, harvest, hunting, recovery, resident Canada goose, survival

INTRODUCTION

Restoration of Canada geese (*Branta canadensis*) is considered a success story of 20th century wildlife management and populations in the US have increased an average of 6.2% per year since the mid-1970s (Schmidt, 2004). Canada geese have become common inhabitants of urban areas due to abundant and stable nesting habitat, plentiful food sources, few predators, and habituation to humans. Canada geese provide recreational opportunities and most residents approve of the presence of Canada geese in their communities but complaints may increase as damage and nuisance problems become more widespread as populations increase (Coluccy et al., 2001; Powell et al., 2004*a*).

Populations of Canada geese have exceeded management objectives in the Atlantic, Mississippi, and Central Flyways and the increasing populations have resulted in nuisance problems (Gabig, 2000). Goose-related problems, including depredation of agricultural crops, airport hazards, fecal contamination of water, and damage to lawns, parks, beaches, and golf courses have increased (Gosser et al., 1997; Coluccy et al., 2004). Control of population growth of temperate nesting Canada geese where they have exceeded public tolerance will be a continuing focus of managers in the future (Moser and Caswell, 2004).

Hunting is the primary cause of mortality in Canada geese (Krohn and Bizeau, 1980) and early September hunting seasons have been implemented to reduce populations of resident Canada geese while causing little or no impact to migratory geese (Gabig, 2000; Coluccy et al., 2004; Vrtiska et al., 2004; Sheaffer et al., 2005). South Dakota was the first state in the Central Flyway to initiate a September season in 1996, followed by North Dakota and Kansas (1999), Oklahoma (2000), and Nebraska (2004; Vrtiska et al., 2004). Relatively few studies have been conducted to determine effects of special hunting seasons on resident Canada geese (Heusmann, 1999; Sheaffer et al., 2005; Dieter et al., 2010*b*) and survival and harvest parameters are important for management decisions (Gabig, 2000; Vrtiska et al., 2004).

In 2004, the Nebraska Game and Parks Commission (NGPC) initiated an early September hunting season to deal with increasing populations of resident Canada geese and damage complaints. The September season has continued through 2010, however no assessment has been made concerning changes in population and harvest demographics in relation to this September season. The objectives of our study were to compare survival, harvest, and recovery rates of Canada geese: 1) 1999–2003 (pre-September season) versus 2004–2010 (September season); 2) banded in southeast Nebraska (September season) versus northeast Nebraska (no September season), 2006–2010; and 3) banded in the Omaha versus the Lincoln metropolitan areas, 2002–2010; 4) by sex. In addition, we determined locations and chronology of both direct and indirect recoveries of geese banded in southeast Nebraska.

STUDY AREA

The September Canada goose season was conducted in 16 counties in southeast Nebraska (Figure 5-1). The Omaha and Lincoln metropolitan areas, located in Douglas, Sarpy, and Lancaster Counties, respectively, were within the bounds of the early Canada goose season. We banded geese at 21 locations in southeast Nebraska including 8 locations in the Omaha area and 13 locations in the Lincoln area. The City of Omaha and associated suburbs cover 380 km² with a population of 865,350 and the City of Lincoln covers 195 km² with a population of 258,379 (US Census Bureau, 2010). The study area of northeast Nebraska included 18 counties (Figure 5-1). We banded geese at 19 locations in northeast Nebraska beginning in 2006. The largest city in the northeast study area was Norfolk, covering 26 km² with a population of 24,210 (US Census Bureau, 2010). We did not band geese at all sites in all years.

METHODS

We captured geese at molting locations by drive trapping during the flightless period of late June and early July (1999–2010). We used plumage characteristics to determine age (hatch-year [HY] or after hatch-year [AHY]) and cloacal examination to determine sex. We fitted all geese with a US Geological Survey band unless previously banded. The length of the early September hunting season was 9 days in 2004 and 2007– 10, 10 days in 2005, and 11 days in 2006. In 2009 and 2010, the early September hunting season opened on Labor Day weekend (September 5 and 4, respectively) and prior to 2009 the season opened the weekend following Labor Day. Through 2009, the daily bag limit was 5 geese, but in 2010 the daily bag was increased to 8 birds per hunter.

We obtained Canada goose banding and recovery data (1999–2010) from the Bird Banding Laboratory in Laurel, MD. We queried only shot birds and labeled recoveries that occurred during the same hunting season as direct and recoveries from after the first hunting season as indirect. We used the Brownie et al. (1985) model in Program MARK (White and Burnham, 1999) to estimate survival (*S*) and recovery (*f*) rates. We used Akaike's information criterion (AIC; Akaike, 1973) to compare models that considered age, sex, location, and year-specific survival and recovery rates for time periods and study areas. We used 2 time periods, pre-September hunting season (1999–2003) and post-initiation of September hunting season (2004–2010) for the analysis of impact of September hunting seasons (*h*) on survival. We constructed 48 models comparing survival and recovery rates of resident Canada geese banded in southeast Nebraska. The global model for the analysis included age (*a*) and year (*t*; *S*(*a*t*) *f*(*a*t*)). We also included a parameter that combined an age class containing non-breeding (*nb*) HY and second-year (SY) geese from the banded HY matrix after survival estimates for separate HY and SY age classes failed. We assumed SY geese were non-breeders (Bellrose, 1976) and compared survival with AHY geese for this model.

We constructed a second set of models that compared survival between 2 locations, southeast Nebraska and northeast Nebraska (2006–2010), which were populations within and outside the September hunt season bounds. We constructed 16 models and the global model for the analysis included location (*l*) and year (S(l*t) f(l*t)). We used latitude 41.40 as the north/south boundary between the 2 areas. We began banding geese in northeast Nebraska in 2006. Age classes were pooled for this analysis to obtain larger sample sizes, thus more reliable survival estimates.

We also examined differences in survival and recovery rates between the Omaha and Lincoln metropolitan areas in Nebraska (2002–2010). We used longitude 96.46 as the

east/west boundary between the 2 areas. We constructed 16 models and the global model for the analysis included location and year (S(l*t) f(l*t)). We began banding birds in the Omaha metro area in 2002. We pooled age classes to obtain larger sample sizes, thus more reliable survival and recovery estimates. We translocated unbanded HY geese from the Omaha area to reduced populations and nuisance issues, so the sample size of the HY cohort was reduced which led us to combine age classes for analysis.

Finally, we constructed models that compared survival and recovery rates by sex for geese banded in southeast Nebraska. We constructed 30 models and combined age classes for this analysis with the global model that included sex (*s*) and year (S(s*t)f(s*t)). We also included the effect of hunt season (*h*) in the sex models. The geese used in this analysis were the same geese used for the pre- and post-hunting season analysis. We combined age classes for this analysis. We included all models that carried 0.01 weights in our tables. We checked for overdispersion in all global models using the median c-hat test in Program Mark (White and Burnham, 1999).

We estimated harvest rates using the direct band return rate divided by the corrected reporting rate (0.763) for geese in Montana, North Dakota, Wyoming, South Dakota, Colorado, Nebraska, and Kansas (Zimmerman et al., 2009) because > 75% of geese banded in southeast Nebraska were recovered in the northern Central Flyway. We determined proportions of direct and indirect band recoveries by state or province and month for AHY, SY, and HY birds. We performed chi-square tests to determine if differences in number of recoveries existed among locations where recoveries were reported and used the proportion of the number of locations divided by the number of band recoveries for those locations as the expected values. In addition, we performed

Fisher's Exact tests (Fisher, 1925) to test for differences in proportion of band recoveries by month for the pre- and post-September hunting periods.

RESULTS

We banded 4,406 AHY and 2,793 HY Canada geese in southeast Nebraska in 1999–2010 and 519 AHY and 1,659 HY Canada geese in northeast Nebraska in 2006– 2010. Hunters recovered 1,443 (33%) AHY geese and 913 (33%) HY geese from the southeast Nebraska cohort and 117 (23%) AHY geese and 391 (19%) HY geese from the northeast Nebraska cohort.

Age and early September hunting seasons

The model *S*(*a*) *f*(*a***t*), which estimated survival by age class and recovery probability by age class and year, was selected as the top model (Table 5-1). The survival estimate (*S*) for AHY geese from the top model was 0.696 (SE = 0.009) and the survival estimate for HY geese (*S'*) was 0.896 (SE = 0.041). Recovery estimates differed by year and age class (Table 5-2). The next best model was S(nb*t) f(a*t), which grouped HY and SY birds into a non-breeding age class and allowed survival to vary yearly. The fourth ranked model in our analysis was the highest ranked model that included September season initiation (*h*) as a parameter, but it carried only 8.6% of the weight and survival confidence intervals for HY (*S*' = 0.863, 95% C.I. = 0.691–0.947 and 0.914, 95% C.I. = 0.739–0.976, pre- and post-hunt, respectively) and AHY geese (*S* = 0.707, 95% C.I. = 0.675–0.736 and 0.694, 95% C.I. = 0.663–0.717, pre- and post-hunt, respectively) overlapped for pre- and post-hunt periods, indicating no differences. We estimated harvest rates for both the pre- and post-hunt periods for both age classes, but confidence intervals overlapped indicating no differences, so we report the mean harvest rate of 0.142 (SE = 0.013) and 0.160 (SE = 0.017) across all years for AHY and HY geese, respectively.

Southeast versus northeast Nebraska

The model $S(.) f(l^*t)$ was selected as the top model to compare survival and recovery rates of resident Canada geese in southeast versus northeast Nebraska (Table 5-3). Survival estimates for southeast and northeast geese did not differ but recoveries differed by location and year (Table 5-4). The second-best model, $S(l) f(l^*t)$, suggested that geese banded in northeast Nebraska had higher survival (0.744, 95% C.I. = 0.666– 0.809) than geese banded in the southeast (0.690, 95% C.I. = 0.635–0.741), but confidence intervals overlapped confirming the results of the top model. Southeast banded geese had a lower estimated harvest rate 0.101 (SE = 0.026) than northeast banded geese 0.159 (SE = 0.023).

Omaha versus Lincoln, Nebraska

The model S(l) f(l*t) was selected as the top model to compare survival and recovery rates of resident Canada geese in the Omaha versus Lincoln metro area (Table 5-5). Survival of Omaha area geese (0.741, 95% C.I. =0.688–0.790) was higher than Lincoln area geese (0.678, 95% C.I. =0.651–0.703). Recovery estimates differed by year and location for both of the top 2 models (Table 5-6). The second-best model was S(.)f(l*t), which had a pooled survival rate for both areas. Mean harvest rate for geese banded in Omaha was 0.111 (SE = 0.010) and mean harvest rate for geese banded in Lincoln was 0.151 (SE = 0.015). The model S(t) f(t) was selected as the top model to compare survival and recovery rates of resident Canada geese by sex (Table 5-7). Survival and recovery estimates differed by year (Table 5-8). The second-best model was S(.) f(t), which combined survival estimates for sex and year. Harvest rates were higher for male Canada geese (0.159, SE = 0.015) than female geese (0.144, SE = 0.012), but no differences (P >0.05) in survival were detected.

Recoveries

Ninety-two percent of all direct recoveries (336 of 399) of AHY geese were in Nebraska (Figure 5-2). Indirect recoveries of AHY banded geese also were concentrated in Nebraska ([75%]; 802 of 1,066). The majority of the remaining recoveries of AHY geese (n = 327) occurred in South Dakota and Kansas. Comparisons of recovery locations differed among states ($\chi^2 = 62.1$ and 61.6, for direct and indirect recoveries, respectively, P < 0.001). We divided the timing of recovery into 2 groups based on the beginning of the September hunting season in 2004. Recoveries shifted from the later months into September after initiation of the early season (Table 5-9) but no differences (P = 0.79) existed between average harvest rates in the pre- and post-hunting periods

The majority of direct and indirect recoveries of HY geese were in Nebraska (98% and 59%, respectively, Figure 5-2). We found differences among recovery locations for the top 5 states for indirect recoveries of HY geese ($\chi^2 = 15.7$, P < 0.005). We did not perform a chi-test for direct recovery locations of HY geese due to lack of geese harvested outside Nebraska. We divided recovery timing of HY geese into 2 groups following the same justification as with AHY birds. We found recoveries of HY geese, both direct (Table 5-10) and indirect (Table 5-11), shifted into September after initiation

of the early season but no differences (P = 0.11) existed between average harvest rates before and after establishment of September hunting seasons in southeast Nebraska. Differences ($P \le 0.0495$) in proportion of band recoveries existed in September– November among AHY, indirect recovery HY, and direct recovery HY geese. Differences also existed in December for AHY geese (P = 0.008) before and after September hunting seasons began.

We detected a dispersal pattern among SY birds as exact numbers of birds were recovered in Nebraska (n = 125) and in states and provinces north of Nebraska (n = 125, Figure 2). Recovery locations of SY birds recovered in areas north of Nebraska were: South Dakota (13%), Manitoba (12%), North Dakota (11%), and Minnesota (6%). Only 19 SY geese (7%) were recovered in states south of Nebraska. We performed a post-hoc survival analysis of SY geese (0.543) and found it was lower than the estimated survival of HY (0.896) or AHY (0.696) geese from the top survival model.

DISCUSSION

Age and early September hunting seasons

We did not detect differences in survival due to initiation of early September hunting seasons for resident Canada geese in southeast Nebraska. Our survival estimates of 0.696 (SE = .009) for AHY and 0.896 (SE = 0.041) for HY geese were lower than reported for this area during 1990–2000 (Powell et al., 2004*b*). Our second-best model combined HY and SY birds into a single non-breeding age class. Few 1-year-old Canada geese attempt to nest (3.9%), but >71% of geese nest at 3 years of age and older (Coluccy et al., 2004). The estimated survival of the non-breeding age class was 0.778, while AHY survival increased slightly from the estimate of our top model (0.696 to 0.710). We concluded the survival rate for the non-breeding cohort was lower than HY geese due to low survival of SY geese. We attempted to assess a model that divided survival estimates into 3 age classes (AHY, SY, and HY) but HY survival was not estimable due to sample size.

Estimates from our top model indicate that HY geese have higher survival than AHY geese. Hatch-year waterfowl typically are more vulnerable to hunting mortality (Bellrose, 1976), but juvenile geese in metropolitan areas that do not disperse during the hatch-year may be experiencing extremely high survival as a result of relatively safe urban environments (Luukkonen et al., 2008; Heller, 2010). Mean survival rates reported for HY Canada geese (0.802) in Illinois, Indiana, and Wisconsin were higher than those of AHY geese (0.722; Sheaffer et al., 2005). Berdeen and Rave (2008) also found similar results in Minnesota (0.818 and 0.608 for HY and AHY, respectively), and geese in Mississippi Flyway had estimated survival rates of 0.784 for HY geese and 0.716 for AHY (Heller, 2010). The number of resident Canada geese that are banded in Nebraska should be increased to improve estimates of survival and recovery. Heller (2010) estimated 1,000–1,500 AHY and 1,800–3,200 HY geese should be banded yearly to increase precision of annual survival estimates and detect temporal changes in recovery rates, but achiving those numbers in Nebraska would be difficult.

Our survival rates were higher for both AHY (0.696) and HY (0.896) birds than Dieter et al. (2010*b*) with the same structure for top models. Our study was conducted in the most highly populated region Nebraska, where hunting access is often restricted, and survival of AHY Canada geese is high in the absence of hunting (Rexstad, 1992). In eastern South Dakota, a more rural environment, annual survival was estimated at 0.523 for AHY and 0.680 for HY geese, and 60% of the band recoveries occurred in the September season (Anderson, 2006; Dieter et al., 2010*b*). Our estimated harvest rate for AHY (0.142) geese was similar to South Dakota but was lower for HY birds (0.160). Hatch-year birds in South Dakota had a harvest rate of 0.22 (Dieter et al., 2010*b*), which was 0.06 higher than our estimated harvest rate. September harvest of Canada geese banded in southeast Nebraska was 29%–43% of the total annual HY band recoveries. September seasons have accounted for ~20% of total harvest of Canada geese in South Dakota, North Dakota, Kansas and Oklahoma (Vrtiska et al., 2004). Urban Canada geese are harvested at very low rates and may have substantially higher survival than rural Canada geese (Balkcom, 2010), which likely is a reason for the higher survival and lower harvest rates we observed.

Southeast versus northeast Nebraska

Survival did not differ between southeast and northeast Nebraska. Northeast Nebraska is more rural and is not within the bounds of the early season. We expected lower survival in northeast Nebraska because the northeast region is more rural and urban areas, which are more prominent in the southeast, act as refuges and survival may be higher in areas where hunting is restricted (Luukkonen et al., 2008) and. Regular dark goose hunting season dates coincide with opening of duck seasons in northeast Nebraska, which should be leading to increased harvest of resident Canada geese. The absence of the early September season may be leading to higher survival than expected in the northeast and due to large populations of geese in the area, so considerations should be made about including northeast Nebraska in early September hunting seasons. In addition, populations of geese in northeast Nebraska may be influenced by geese moving away from South Dakota or Minnesota in September due to hunting pressure. Increased seasonal populations of migratory geese may reduce the probability of harvest of geese banded in northeast Nebraska. Marked geese in South Dakota made southern migrations >100 km in response to September hunting seasons (Dieter et al., 2010*a*).

Omaha versus Lincoln, Nebraska

Survival was higher in Omaha than Lincoln. The Omaha metro area covers a larger area than the Lincoln metro area, including more parks, ponds, golf courses, and other habitat favorable to urban Canada geese. Increasing bag limits and season lengths had little impact on urban geese in Missouri (Coluccy et al., 2004). We conclude that birds banded in the Omaha metro area do not experience the same level of hunting pressure as birds banded in the Lincoln metro area, which is supported by our estimated harvest rates and survival estimates.

Sex

We did not expect differences in survival due to sex, and model results confirmed that expectation, but harvest rates were higher for males than females. The plumage of Canada geese is not sexually dimorphic, so we did not expect hunter selection, but Imber (1968) suggested males were 1.15 times more vulnerable to hunting due to leadership of flights or because of larger size. The small differences in hunting vulnerability reported by Imber (1968) may not be evident with the number of geese banded in our study and differences in size may not be clear in flocks with mixed ages and sexes. Estimated annual survival for neck-collared female geese, banded in Lancaster County, Nebraska, was 0.49 in 1991–1994 (Groepper et al., 2008), which was much lower than our estimate of survival (0.702) of female geese. Neck collars may negatively influence survival (Samuel et al., 1990; Castelli and Trost, 1996; Schumtz and Morse, 2000; Alisauskas and

Lindberg, 2002). Canada geese have few sources of post-fledging mortality other than hunting (Krohn and Bizeau, 1980). In urban environments, predators are lacking and mortality during the nesting season likely is diminished. Male geese guard nests and incubating pairs aggressively defend nests from predators (Bellrose, 1976). Gosser and Conover (1999) reported no mortality of resident Canada geese incubating nests, suggesting mammalian predation was low.

Recoveries

Analysis of band recoveries from 1999 to 2010 revealed that the majority of AHY and HY geese banded in Nebraska were recovered in Nebraska. In 1990–2000, 92% of geese banded in Lancaster County were directly recovered in Nebraska (Powell et al. 2004*b*). Hatch-year birds likely remain in family groups through the year so recoveries may be influenced by the habits of AHY geese (Hanson, 1962; Bellrose, 1976). Eightytwo percent of AHY and 73% of HY Canada geese banded in South Dakota were directly recovered in South Dakota as well as 77% of AHY and 64% of HY indirect recoveries (Dieter et al., 2010*b*). A high proportion of in-state recoveries are typical when populations of geese delay departure from banding areas (Raveling, 1978) or in the case of resident geese, rarely leave banding areas. An increase in the proportion of banded birds harvested in September likely caused high numbers of direct recoveries of HY birds in Nebraska.

Second-year geese as well as failed or non-nesting AHY geese we banded participated in molt migrations. Sub-adult and failed nesting adult Canada geese are known to undergo molt migration (Davis et al., 1985; Lawrence et al., 1998; Abraham et al., 1999; Luukkonen et al., 2008; Dieter and Anderson, 2009). Molt migrations are characterized by movements during the spring and fall seasons to and from high resource locations for the purpose of molting (Zicus, 1981; Abraham et al., 1999). Geese molt their flight feathers in northern locations during the months of June and July and afterward move southward to breeding grounds in September–November (Abraham et al., 1999; Luukkonen et al., 2008). In South Dakota, 56% of non-breeders and 81% of unsuccessful breeders participated in molt migrations (Dieter and Anderson, 2009). Only non-breeding geese molt migrate, breeding geese typically remain at nesting areas to raise goslings (Salomonsen, 1968). Molt migration may be less common for urban geese. Incidence of migration of geese that nested in urban parks in Michigan was lower (23%) than birds nesting in other classes of land use (87%; Luukkonen et al., 2008). Reported distances of molt migrations range from 40 km in Utah (Martin, 1964) to 2,100 km in South Dakota (Anderson, 2006). Second-year Canada geese had reduced survival in our study. Molt migrant geese may have reduced survival compared with birds that remain in breeding areas due to greater hunting and natural mortality (Ogilvie, 1978; Lawrence et al., 1998).

MANAGEMENT IMPLICATIONS

Results from our survival analysis indicate that early September hunting seasons for resident Canada geese in Nebraska did not reduce survival, however survival also has not increased in southeast Nebraska since 1990. We believe the population may be growing slightly faster than mortality (M. Vrtiska, NGPC, unpublished data) and initiation of September seasons is keeping population expansion in-check. Expansion of the early season zone to include northeast Nebraska as well as a shift west may be warranted to harvest birds dispersing away from saturated urban areas. Harvest of geese outside the Omaha and Lincoln areas may have little effect on populations that are causing most urban damage. Urban hunts could address these issues, but it is unlikely that they would be accepted by the public (Coluccy et al., 2001) and logistically urban hunts would be difficult to manage. Other methods of population control must be employed to stem damage and nuisance complaints when hunting alone is either not meeting populations goals or is unacceptable to the public.

The NGPC and permitted individuals currently participate in egg oiling (M. Vrtiska, NGPC, personal communication). Reproductive control efforts must be nearly complete to be effective: if a small number of eggs are not treated, the resulting recruitment may be sufficient to offset decreased production from oiled eggs (Smith et al., 1999). Simulations indicated a flock of urban Canada geese could remain stable if 72% of eggs were removed annually and if 95% of eggs were removed, the population would decrease by 25% in 10 years (Barnard, 1991). Coluccy et al. (2004) reported that 71% of nests would need to be removed annually over a 10-year period to stabilize the population of Canada geese in Missouri.

Translocation of problem geese is an option, but adult geese have strong homing instincts and may return (Keefe, 1996). Twelve of 66 (18%) AHY, female, neck-collared Canada geese translocated 500 km in Nebraska returned to banding areas within 2 years (Groepper et al., 2008). Twenty-five percent of marked Canada geese translocated 150 km in New York returned to their initial capture site within 10 months, but were harvested at higher rates (24%) during September than AHY geese not translocated (7%; Holevinski et al., 2006). In addition, translocated juveniles were harvested at higher rates (23%) than juveniles that were not translocated (5%; Holevinski et al., 2006). After hatch-year and HY geese were released together in this study. We recommend HY birds not be released with AHY birds because goslings often have not imprinted on their environment and are more likely to stay at the release site if AHY birds are not present (Gosser et al., 1997).

Non-lethal chemical repellents, hazing methods, and exclusion devices have been tested on resident Canada geese. Limitations of repellents include cost of the chemical and labor and many have mixed or poor efficacy (Smith et al., 1999). Chemical repellents may not completely stop geese from using an area. Hazing techniques usually are accepted by the public (Smith et al., 1999), but habituation of birds can occur (Ruger, 1985; Summers, 1985; Aubin, 1990). Urban geese are accustomed to a variety of sights and sounds associated with humans and are more difficult to haze than migratory geese (Fairaizl, 1992; Swift, 1998). Non-lethal management alternatives can be expensive and generally are ineffective for long-term, widespread control (Coluccy et al., 2001). We recommend non-lethal control methods where other methods, such as hunting, are not feasible. These methods often are more acceptable to the public than lethal control methods.

Resident Canada geese can be controlled using lethal methods. Sharp shooting or capture and euthanasia may be necessary where hunting is not allowed and other methods only temporally solve problems. Development of effective lethal management programs has been hampered by ethical concerns regarding treatment of animals, public awareness, fear of firearms, and perception of hunters and hunting (Shaw, 1977; Duda et al., 1998). Lethal methods to control populations of geese in urban areas may not be socially acceptable. Individuals may be willing to accept lethal alternatives if they clearly understand goose-related problems and agencies demonstrate lethal methods are the most feasible means of controlling problems (Coluccy et al., 2001). The public also may be more accepting of euthanasia if meat is donated to the needy. A study in Minnesota found the price to process Canada geese for use at local food banks was \$18–\$25 per goose (Keefe, 1996), so costs associated may be prohibitive for state agencies. Issues of permitting donation of wild game meat or steel shot in birds need to be explored before implementation of such a program. In Missouri, estimated removal of 14% of AHY geese (n = 7,732) and 71% of HY geese (n = 24,665) annually was required to meet population managements objectives (Coluccy et al., 2004). We recommend lethal control methods, other than hunting, when non-lethal control methods have proven ineffective, problems have outgrown public tolerance, or human health and safety are an imminent concern.

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Table 5-1. Summary of models used to compare survival and recovery rates of resident Canada geese banded in southeast Nebraska by age and effects of early hunting seasons, 1999–2010.

Model	AIC	Δ AIC	Weight	Likelihood	Parameters
$\{S(a) f(a^*t)\}$	16,404	0.00	0.374	1.000	26
$\{S(nb)f(nb*t)\}$	16,405	0.54	0.286	0.764	26
$\{S(a^*t)f(t)\}$	16,406	1.61	0.168	0.448	34
$\{S(a^*h)f(a^*t)\}$	16,407	2.93	0.086	0.231	28
$\{S(a) f(t)\}$	16,409	4.65	0.037	0.098	14
$\{S(a^{*t})f(a^{*t})\}$ global	16,409	4.85	0.033	0.088	46
$\{S(a*h)f(t)\}$	16,410	6.28	0.016	0.043	16

S = survival estimate, f = recovery estimate, a = age (after-hatch year or hatch-year), h = hunt season (pre- or post-hunting season), nb = non-breeding age class including hatch-year and second-year geese, t = year

Parameter	Year	Estimate	SE	Upper 95% CI	Lower 95% CI
S^1		0.696	0.009	0.679	0.713
f	1999	0.112	0.011	0.093	0.136
f	2000	0.159	0.012	0.137	0.183
f	2001	0.080	0.008	0.066	0.096
f	2002	0.093	0.008	0.079	0.109
f	2003	0.122	0.009	0.106	0.140
f	2004	0.130	0.010	0.111	0.150
f	2005	0.138	0.009	0.121	0.157
f	2006	0.108	0.008	0.094	0.124
f	2007	0.123	0.009	0.107	0.142
f	2008	0.090	0.008	0.076	0.107
f	2009	0.120	0.010	0.102	0.140
f	2010	0.076	0.007	0.063	0.091
S'^2		0.896	0.041	0.786	0.953
f	1999	0.143	0.032	0.091	0.217
f	2000	0.112	0.028	0.068	0.179
f	2001	0.131	0.031	0.082	0.203
f	2002	0.057	0.019	0.029	0.109
f	2003	0.077	0.027	0.038	0.151

Table 5-2. Estimates of survival (*S*) and recovery (*f*) from the model S(a) f(a*t) of Canada geese banded in southeast Nebraska, 1999–2010.

Parameter	Year	Estimate	SE	Upper 95% CI	Lower 95% CI
f	2005	0.202	0.019	0.167	0.243
f	2006	0.094	0.196	0.062	0.140
f	2007	0.124	0.019	0.090	0.167
f	2008	0.094	0.015	0.069	0.128
f	2009	0.132	0.020	0.098	0.176
f	2010	0.113	0.017	0.083	0.151

¹ Survival estimate for after hatch-year Canada geese

² Survival estimate for hatch-year Canada geese

Model	AIC	ΔΑΙΟ	Weight	Likelihood	Parameters
$\{S(.)f(l^*t)\}$	7,209.6	0	0.454	1.000	11
$\{S(l)f(l^*t)\}$	7,210.2	0.62	0.334	0.734	12
$\{S(l^*t)f(l^*t)\}$ global	7,212.2	2.63	0.122	0.269	18
$\{S(t)f(l^*t)\}$	7,212.9	3.29	0.088	0.193	14

Table 5-3. Summary of models used to compare survival and recovery rates of resident Canada geese banded in southeast versus northeast Nebraska, 2006–2010.

S = survival estimate, f = recovery estimate, l = location (southeast or northeast Nebraska), t = year, . = location/year combined parameter

Region	Year	Parameter	Estimate	SE	Lower 95% CI	Upper 95% CI
Combined		S	0.712	0.022	0.666	0.752
Southeast	2006	f	0.081	0.011	0.063	0.104
	2007	f	0.114	0.011	0.094	0.139
	2008	f	0.099	0.010	0.080	0.121
	2009	f	0.166	0.017	0.136	0.202
	2010	f	0.151	0.015	0.124	0.182
Northeast	2006	f	0.148	0.027	0.102	0.210
	2007	f	0.136	0.015	0.109	0.168
	2008	f	0.146	0.013	0.122	0.174
	2009	f	0.157	0.015	0.130	0.188
	2010	f	0.061	0.006	0.050	0.075

Table 5-4. Estimates of survival (*S*) and recovery (*f*) from the model S(.) f(l*t) of Canada geese banded in southeast and northeast Nebraska, 2006–2010.

Table 5-5. Summary of models used to compare survival, harvest, and recoveries of resident Canada geese banded in the Omaha versus Lincoln metro areas, Nebraska, 2002–2010.

Model	AIC	ΔΑΙΟ	Weight	Likelihood	Parameters
$\{S(l)f(l^*t)\}$	9,952.1	0	0.731	1.000	20
$\{S(.)f(l^*t)\}$	9,955.1	2.97	0.166	0.227	19
$\{S(.)f(t)\}$	9,957.7	5.56	0.045	0.062	10
$\{S(l)f(t)\}$	9,959.1	6.99	0.022	0.030	11
$\{S(t)f(l^*t)\}$	9,959.8	7.66	0.016	0.022	26

S = survival estimate, f = recovery estimate, l = location (Omaha or Lincoln, Nebraska), t = year, . = location/year combined parameter

Location	Year	Parameter	Estimate	SE	Lower 95% CI	Upper 95% CI
Omaha		S	0.712	0.026	0.688	0.790
	2002	f	0.125	0.038	0.067	0.220
	2003	f	0.109	0.018	0.078	0.150
	2004	f	0.114	0.016	0.086	0.149
	2005	f	0.105	0.015	0.079	0.137
	2006	f	0.071	0.012	0.050	0.10
	2007	f	0.104	0.015	0.078	0.138
	2008	f	0.068	0.012	0.047	0.096
	2009	f	0.123	0.021	0.087	0.169
	2010	f	0.075	0.014	0.052	0.107
Lincoln		S	0.678	0.013	0.651	0.703
	2002	f	0.070	0.011	0.051	0.096
	2003	f	0.138	0.013	0.114	0.165
	2004	f	0.134	0.013	0.111	0.163
	2005	f	0.170	0.013	0.146	0.200
	2006	f	0.109	0.009	0.092	0.128
	2007	f	0.140	0.011	0.120	0.164
	2008	f	0.110	0.010	0.091	0.130
	2009	f	0.136	0.011	0.115	0.159
	2010	f	0.098	0.009	0.082	0.118

Table 5-6. Estimates of survival (*S*) and recovery (*f*) from the model S(l) f(l*t) of Canada geese banded in the Omaha and Lincoln metro areas, Nebraska, 2002–2010.

Table 5-7. Summary of models used to compare survival and recoveries of resident Canada geese banded in southeast Nebraska by sex, 1999–2010.

Model	AIC	ΔΑΙΟ	Weight	Likelihood	Parameters
$\{S(t)f(t)\}$	16,874.4		0.970	1.000	23
$\{S(.)f(t)\}$	16,882.3	7.94	0.018	0.019	13
$\{S(s)f(t)\}$	16,883.3	8.91	0.011	0.012	14

S = survival estimate, f = recovery estimate, s = sex (male or female), t = year, . =

sex/year combined parameter

Parameter	Year	Estimate	Standard Error	Lower 95% C.I.	Upper 95% C.I.
S	2000	0.708	0.055	0.591	0.803
	2001	0.608	0.051	0.505	0.071
	2002	0.756	0.057	0.629	0.850
	2003	0.816	0.064	0.659	0.911
	2004	0.646	0.055	0.533	0.745
	2005	0.657	0.050	0.553	0.749
	2006	0.786	0.060	0.646	0.881
	2007	0.711	0.068	0.563	0.825
	2008	0.630	0.069	0.489	0.782
	2009	0.693	0.087	0.503	0.834
	2010	0.420	0.067	0.297	0.554
f	1999	0.110	0.011	0.091	0.133
	2000	0.154	0.012	0.132	0.180
	2001	0.095	0.009	0.079	0.113
	2002	0.089	0.008	0.075	0.106
	2003	0.113	0.009	0.097	0.132
	2004	0.124	0.010	0.105	0.145
	2005	0.161	0.010	0.144	0.181
	2006	0.108	0.008	0.092	0.125

Table 5-8. Estimates of survival (*S*) and recovery (*f*) from the model S(t) f(t) of Canada geese, by sex¹, banded in southeast Nebraska, 1999–2010.

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Parameter	Year	Estimate	SE	Lower 95% CI.	Upper 95% CI.
f	2007	0.123	0.010	0.104	0.145
	2008	0.098	0.009	0.081	0.118
	2009	0.168	0.017	0.138	0.203
	2010	0.151	0.015	0.124	0.182

¹Results of the model did not show differences in survival due to sex, so survival estimates are combined.

Table 5-9. Proportion of combined direct¹ and indirect² recoveries of after hatch-year Canada geese banded in southeast Nebraska, before and after establishment of September Canada goose hunting seasons in 2004.

Period	Year	Sept	Oct	Nov	Dec	Jan	Feb
Pre-hunt	1999	0	36	10	27	0	0
	2000	8	26	37	61	14	1
	2001	16	21	15	19	14	4
	2002	22	17	32	22	19	0
	2003	8	46	41	38	26	3
		0.09*	0.25*	0.23*	0.29*	0.13	0.01
Post-hunt	2004	25	20	18	29	30	0
	2005	54	23	33	49	42	1
	2006	56	18	23	16	20	4
	2007	35	15	22	28	19	1
	2008	23	14	13	15	20	2
	2009	22	13	7	15	14	0
	2010	27	7	7	17	24	2
		0.29*	0.13*	0.15*	0.20*	0.20	0.01

* Differences exist between pre- and post-hunt time periods (P < 0.05)

Table 5-10. Proportion of direct recoveries¹ of hatch-year Canada geese banded in southeast Nebraska, before and after establishment of September Canada goose hunting seasons in 2004.

Period	Year	Sept	Oct	Nov	Dec	Jan
Pre-hunt	1999	0	8	1	6	0
	2000	0	2	4	4	0
	2001	4	0	2	0	0
	2002	1	2	4	0	0
	2003	0	0	6	0	1
		0.11*	0.27*	0.38*	0.22	0.02
Post-hunt	2004	6	7	3	5	0
	2005	37	17	4	19	0
	2006	16	1	1	1	0
	2007	7	2	8	17	0
	2008	7	3	10	8	0
	2009	12	2	3	15	0
	2010	21	4	2	11	0
		0.43*	0.14*	0.12*	0.31	0

Direct recoveries of hatch year Canada Geese

* Differences exist between pre- and post hunt time periods (P < 0.05)

¹Direct recoveries occur the same year the goose was initially banded

Table 5-11. Proportion of indirect recoveries¹ of hatch-year Canada geese banded in southeast Nebraska, before and after establishment of September Canada goose hunting seasons in 2004.

Period	Year	Sept	Oct	Nov	Dec	Jan	Feb
Pre-hunt	1999	0	8	1	6	0	0
	2000	0	3	12	10	1	0
	2001	7	2	6	2	2	0
	2002	4	3	9	5	8	0
	2003	9	19	8	4	2	0
		0.15*	0.27*	0.27*	0.21	0.10	0
Post-hunt	2004	25	14	7	13	3	0
	2005	56	27	13	30	12	0
	2006	39	18	13	13	7	0
	2007	46	21	21	37	9	3
	2008	27	14	23	15	6	0
	2009	34	25	15	30	15	0
	Hunt %	0.35*	0.18*	0.13*	0.21	0.10	0.01

Indirect Recoveries of Hatch Year Canada Geese

* Differences exist between pre- and post hunt time periods (P < 0.05)

¹ Indirect recoveries occur in years after the first hunting season



Figure 5-1. Map of the study areas in eastern Nebraska, including the northeast study area and the southeast early September Canada goose hunting zone in the inset (2004–2010).



Figure 5-2. Number and locations of direct (DR) and indirect recoveries (IR) of after hatch-year (AHY), hatch-year (HY), and second-year (SY) Canada geese banded in southeast Nebraska, 1999–2010.