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Role of bird movements in the epidemiology of West Nile and avian influenza virus

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Abstract: Avian influenza virus (AIV) is influenced by site fidelity and movements of bird hosts. We examined the movement ecology of American crows (*Corvus brachyrhynchos*) as potential hosts for West Nile virus (WNV) and greater white-fronted geese (*Anser albifrons frontalis*) as potential hosts for AIVs. Research was based on radio-telemetry studies conducted in the Central Valley of California, USA. While crows were restricted to a small area of only a few square kilometers, the distribution of the geese encompassed the northern Central Valley. The crows used 1.5 to 3.5 different roosting areas monthly from February through October, revealing lower roost fidelity than the geese that used 1.1 to 1.5 roosting areas each month from November through March. The crows moved a mean distance of 0.11 to 0.49 km/month between their roosting sites and 2.5 to 3.9 km/month between roosting and feeding sites. In contrast, the geese moved 4.2 to 19.3 km/month between roosting areas, and their feeding range varied from 13.2 to 19.0 km/month. Our comparison of the ecological characteristics of bird movements suggests that the limited local movements of crows coupled with frequent turnover of roosts may result in persistence of focal areas for WNV infection. In contrast, widespread areas used by geese will provide regular opportunities for intermixing of AIVs over a much greater geographic area.

Key words: avian influenza, epidemiology, disease ecology, human–wildlife conflicts, migratory birds, movement ecology, West Nile virus

INFECTIOUS DISEASES are important determinants of fitness, reproductive success, and population dynamics of wildlife (Daszak et al. 2000, Tompkins et al. 2011). Globalization, agricultural intensification, as well as habitat loss and fragmentation, have increased the incidents of emerging infectious diseases giving rise to geographic invasion by pathogens, epizootics, and epidemics (Daszak et al. 2000, Daszak 2005, Wilcox and Colwell 2005, Thomson et al. 2006). Increased interaction at the wildlife–livestock–human interface has facilitated the emergence and spread of diseases. In spite of their global significance to the health of wildlife, domestic animals, and humans, quantitative studies addressing the ecological aspects of pathogen transmission are limited (Daszak et al. 2000, Hudson et al. 2002, Collinge and Ray 2006).

Many diseases that are transmissible between humans and wild birds have gained considerable attention in recent years from both scientific and sociological perspectives (Collinge and Ray 2006, Altizer et al. 2011). Examples include the spread of West Nile Virus (WNV) across North America after its introduction in New York in 1999 (Kramer et al. 2008) and emergence of avian influenza viruses (AIV), such as highly pathogenic avian influenza (HPAI), H5N1, which arose in China in 1997 and spread across Eurasia (Hulse-Post et al. 2005, Takekawa et al. 2010). Although much has been learned about the epidemiology

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and genetics of these pathogens over the past decade, significant gaps in our understanding of how the ecology of wild birds influences pathogen transmission still remain.

Movement ecology is a rapidly evolving discipline that highlights the importance of movement of organisms on the structure and functioning of ecosystems (Holyoak et al. 2008, Nathan et al. 2008). Movement of an organism is determined by its internal state (physiological factors prompting movement), capacity to move and navigate, and a suite of external factors that influence movement (Nathan et al. 2008). Resident dabbling ducks, such as green-winged teal (*Anas crecca*), tend to use distinct diurnal roosting areas and nocturnal feeding areas, with strategies to switch between local sites to optimize resource utilization (Guillemain et al. 2010). Populations of birds may also have resident, migrant, and partial migrant populations (Altizer et al. 2011). For example, larger, dominant individuals of tropical kingbirds (*Tyrannus melancholicus*) may become partial migrants to take advantage of resources farther from their local home range (Jahn et al. 2010). Site fidelity is central to partial and full migration strategies, and food and water availability are important determinants of site fidelity in many species (Nathan et al. 2008). Residents, migrants, or partial migrants often are characterized by spatially and temporally variable aggregations. Quantitative information on these aggregation patterns is limited.

Pathogen transmission, through direct contact or through the aid of arthropods, is greatly enhanced by the aggregation of birds (Clayton and Moore 1997, Neilson and Reisen 2007, Nielsen et al. 2008, Boyce et al. 2009, Altizer et al. 2011). Roosting, feeding, and staging areas are all important aggregation sites for many birds. In resident species (or populations) with relatively short dispersal movements, such as the American crow (*Corvus brachyrynchos*) or American robin (*Turdus migratorius*), evidence suggests that roosting sites are likely to create disease foci connected by movement of birds between roosts that could lead to epidemics (Ward et al. 2006, Diuk-Wasser et al. 2010). Spread of disease by resident species would be a function of the size of bird populations and their foraging or dispersive movements (Diuk-Wasser et al. 2010). In contrast, aggregations of migratory birds at roosting sites can create similar foci that actually help disperse the disease over greater distances. The congregation of birds at breeding, wintering, and stopover sites facilitates the inter- and intra-specific transmission of pathogens (Boyce et al. 2009, Altizer et al. 2011). However, persistence of the pathogens in the environment is a critical factor (Stallknecht et al. 1990, Brown et al. 2007, Swayne 2008, Lebarbenchon et al. 2009), and the extent to which pathogens persist in the environment in these aggregation sites may help to determine the local persistence and spread of disease. Species with both resident and migrant individuals could facilitate both local persistence and periodic spread of diseases. Establishing linkages among roosting and feeding areas to pathogen transmission requires careful study of bird movement between these areas.

We chose 2 different viral disease systems, WNV and AIV, to examine questions on the impact of avian ecology on pathogen transmission. West Nile virus was introduced into the USA during 1999 and is a mosquito-borne *Flavivirus* native to Eurasia and Africa (reviewed by Kilpatrick et al. 2007, Kramer et al. 2008). The success of WNV in exploiting many areas at the local and landscape levels that have facilitated its spread across North America and into South America has been driven by its exploitation of many bird host species and the diverse, moderately competent mosquito fauna (e.g., *Culex pipiens*, *C. tarsalis*, *C. quiquefasciatus*). This has resulted in the morbidity and mortality of many wild bird species (especially Corvidae), as well as mammals, including horses and humans (Komar et al. 2003, Kramer et al. 2008). First detected in California in 2003 (Reisen et al. 2004), WNV has caused significant mortality in many bird species, including the yellow-billed magpie (*Pica nuttalli)*, which is endemic to northern California (Wheeler et al. 2009). West Nile virus ecology is linked with above-threshold temperatures needed for viral extrinsic incubation, juxtaposition of mosquito vector and avian host distribution, and the presence of bridging vectors (feeding on birds and mammals; Nielsen et al. 2008, Kramer et al. 2008, Diuk-Wasser et al. 2010). In California, *Culex* mosquitoes serve as maintenance, amplification, and bridge vectors (Reisen et al. 2004). The extent to which bird movements

influence the ecology of WNV is not well-known.

In comparison, numerous subtypes of AIVs circulating among wild waterfowl are found in North America (Webster et al. 1992). Although generally causing only mild disease in wild ducks (Jourdain et al. 2010), the AIV subtypes have a tendency to evolve quickly and become highly pathogenic, especially in poultry or mixed bird markets (Panigrahy et al. 2002, Duan et al. 2007, Boyce et al. 2009). Emergence of HPAI H5N1 in the late 1990s and the associated mortality of poultry, wild waterfowl, zoo animals, and humans has increased concerns about threats of a global pandemic (reviewed by Gauthier-Clerc et al. 2007, Takekawa et al. 2010). Of significance to North America is the repeated emergence of the HPAI H5N2 subtype in poultry in Mexico and some southern states in the USA (Horimoto et al. 1995, Panigrahy et al. 2002). To date, H5N2 is the only subtype of HPAI virus that has been documented to be carried over large geographic regions without causing disease in the host (Gaidet et al. 2008).

We examined site fidelity and local movements of American crows in relation to WNV transmission and greater white-fronted geese (*Anser albifrons frontalis*) with respect to AIV transmission. The objective of this study was to quantify spatial distribution patterns of avian hosts to better understand the potential role of movement ecology in transmission, persistence, and spread of these 2 zoonotic pathogens.

Study area

We conducted movement studies at 2 scales within California's Central Valley (CCV). At the regional scale, CCV is composed of 9 basins (U.S. Fish and Wildlife Service 1978, Central Valley Habitat Joint Venture Implementation Board 1990). It supports 95% of California's rice in the Butte, Colusa, American, Sutter, Yolo, and Delta basins of the northern CCV area known as the Sacramento Valley (Tippet and Hettinger 1986). Rice production in CCV ranges annually from 140,000 to 180,000 ha (Hill et al. 1992) and has some of the highest yields in the world (Miller et al. 1989, Brouder and Hill 1995). In addition to rice habitats, there are numerous federal and state waterfowl refuges and private reserves in the CCV that comprise about 191,000 ha (J. P. Fleskes, U.S. Geological Survey, unpublished data). At the local scale, the city of Davis (38.54°N, 121.74°W) covers 27.1 km^2 and is located in lower Yolo County 22 km west of Sacramento; it has a human population of 64,000. It is surrounded by mixed agriculture consisting of fodder, row crops, and orchards.

Materials and methods

American crow movements

We captured American crows with a ground net-launcher (Coda Enterprises Inc., Mesa, Ariz.) in Davis, California, between October 2004 and December 2006. Capture methods were approved by Institutional Animal Care and Use Committee of the University of California–Davis. Trapping sites were located at the Center of Equine Health on the University of California campus. We baited each trapping site with hard-boiled eggs and dog kibble (Verbeek and Caffrey 2002) for 7 to 10 consecutive days to habituate crows to feeding (Ingold 2003). We also stationed a wood replica of the ground net-launcher 1 m away from the bait. After a habituation period, we set and triggered the net-launcher, either manually or remotely, to capture birds (Ingold 2003).

We captured crows in the morning (0700 to 1000 hours) or late afternoon (1500 to 1700 hours) based on their seasonal movements and foraging strategies. This capture method was most successful during mid-morning and late afternoon after birds had returned from foraging sites and before they returned to their night roosts (Stouffer 2004). Once birds were captured, they were placed into individual bird bags and processed. We examined and weighed each bird, collected oral and cloacal swabs, plucked 2 contour feathers, and drew blood. We then banded each bird, fitted each with a radio transmitter (Advanced Telemetry Systems Inc., Isanti, Minn.) and released it immediately.

Radio transmitters were attached with backpacks made of 0.6-cm Teflon® ribbon and secured by crimping 0.64-cm copper tubing. Transmitters (Advanced Telemetry Systems Inc., Isanti, Minn.) weighed 11.2 g with an expected battery life of 6 months. A mortality signal was triggered after 6 hours without movement to allow for possible carcass retrieval. We tracked birds at least once every 72 hours and every 24 hours, when possible. We monitored the birds

from vehicles equipped with a Yagi antenna receiving system (Gilmer et al. 1981). During the months of June through August 2005, birds not located from the ground were searched for using fixed-winged aircraft (Gilmer et al. 1981). We developed a grid system and map to document bird locations during the day and at night roost sites. We created a driving route so that each grid on the map would be equally represented during daytime searches. We used a smaller grid map and shorter driving scheme to encompass the night roosting sites, which were located in Davis.

The sample size of radio-tracked crows (n = 20) was maintained for the entire period by capturing new individuals to replace those that had been lost or had died. Thus, we captured 55 crows and fitted them with radio transmitters. Telemetry locations allowed us to calculate movement metrics, including: (a) roost-to-roost movements from roost locations collected on consecutive days; (b) roost-to-feeding location movements from roost and daytime locations on the same date; and (c) the number of roosts used by month. We used telemetry data collected between February and October 2005 for all analyses that coincided with peak WNV activity.

WNV surveillance

We collected oral and cloacal swabs (using sterile cotton-tip applicators) for WNV testing. A subsample of these swabs was tested with the Rapid Analyte Measurement Platform (RAMP) system, which is a quantitative, on-site antigen-antibody test (Response Biomedical Corporation Burnaby, B.C., Canada). We placed the remaining swab samples in viral transport media for future testing by reverse-transcriptase polymerase chain reaction assay (RT-PCR). Contour feather pulp collected from live crows was stored for WNV isolation and RT-PCR assay analysis (Docherty 2004). We submitted the sera obtained from blood samples to the Center of Vector-Borne Diseases (CVEC), University of California–Davis, for screening of western equine encephalitis virus (WEEV) and WNV-Saint Louis encephalitis virus (SLEV) antigens with enzyme immunoassay (EIA; Reisen et. al. 2004). We used endpoint plaque-reduction neutralization test (PRNT) to separate *Flavivirus* (WNV and SLEV) antibodies (Brault 2004, Reisen et. al. 2004).

We retrieved marked birds that died within 24 to 48 hours whenever possible. We geo-referenced the retrieval locations and submitted the carcasses for necropsy and histopathology. Carcasses were incorporated into the California Department of Health Services dead bird WNV surveillance program (modeled after the state of New York's program) at the Center for Animal Health and Food Safety (CAHFS; Eidson 2001, Nasci 2002). We necropsied the carcasses, submitted tissues for histopathology, and collected kidney swabs for RT-PCR (Johnson et al. 2001). We categorized as "lost" the carcasses that were not recovered, had failed transmitters, or birds that were undetected during tracking.

Greater white-fronted goose movements

We herded molting geese into corral traps (Cooch 1953) with aircraft on the central Yukon-Kuskokwim Delta (61.82°N, 165.82°W) of Alaska, USA, near the Kashunuk and Manokinak rivers, from June 21, 1998, to July 31, 1998, and from July 8, 1999, to August 5, 1999 (Ackerman et al. 2006). We determined the age and sex of all captured geese, weighed and measured the adults (Orthmeyer et al. 1995), and radio-marked adult females. We marked geese with metal leg bands and a 30-g solar radio-transmitter (Advanced Telemetry Systems) glued to a yellow plastic neck collar (Spinners Plastics, Springfield, Ill.) individually identified with black digits (Ely 1993, Ely and Takekawa 1996). Transmitter life was about 24 months for solar-powered radio-transmitters.

We tracked geese as they arrived to CCV wintering grounds from trucks and fixed-wing aircraft equipped with dual 4-element Yagi antenna systems (Advanced Telemetry Systems). Trucks were equipped with null-peak systems (AVM Instrument Company, Livermore, Calif.) to accurately determine bearings, whereas the aircraft had left–right systems (Advanced Telemetry Systems) to circle and pinpoint signals on either side of the plane (Gilmer et al. 1981). Geese were located daily from trucks between November 1 through March 15 and monthly by aircraft from November 1 to April 15 of each year (Ely and Takekawa 1996). For each location by truck, we obtained 2 bearings within several minutes to minimize movement error.

White-fronted geese generally fly from roosting to feeding sites each morning and evening to feed in agricultural fields (Ely 1990, 1992; Krapu et al. 1995). On the basis of our field observations, we classified locations collected during morning (0531 to 1030 hours) and evening (1531 to 2230 hours) as feeding sites and midday (1031 to 1530 hours) and night (2231 to 0530 hours) as roosting sites. We verified feeding and roosting locations with direct observations whenever possible, or we recorded the main behavior associated with a time period when we could not observe the goose during triangulation. Rather than visually identifying the radio-marked individual within a large flock located at the point of triangulation, we assumed that the behavior of the radio-marked goose was similar to the behavior of the main flock.

AIV surveillance

We sampled harvested waterfowl at Sacramento National Wildlife Refuge (NWR) in Glenn County (39.41°N, 122.17°W) and Conaway Ranch Duck Club in Yolo County (38° 38′52″N, 121° 40′1″W) in the CCV (for more details, see Hill et al., in press). Greater white-fronted geese were sampled when hunters exited the check stations with sampling taking place up to 3 times per week between October 2007 to January 2008 and October 2008 to January 2009. We inserted a rayon-tipped swab (MicroPur™, PurFybr Inc., Munster, Ind.) into the bird's cloaca to collect AIV samples. The tip of the swab was removed and preserved in cryovial tubes (Remel Inc., Lenexa, Kan.) containing viral transport media. We kept the samples on ice for up to 8 hours before storage in a -70°C freezer prior to laboratory analysis. We screened samples for AIV by virus isolation in embryonating chicken eggs followed by testing for hemagglutinating activity with chicken red-blood cells. We conducted virus isolation without rRT-PCR screening to minimize refreezing samples and maximize the likelihood of growing viral subtypes for sequencing.

In brief, we inoculated 150 µl of viral transport medium (VTR) into the allantoic cavity of 9- to 11-day-old embryonating specific pathogen-free (SPF) chicken eggs (Charles River Avian Vaccine Services, Wilmington, Mass.) and incubated at 37.5°C for 6 days or until embryo death, as detected by daily candling. The virus allantoic fluid (VAF) from live embryos was tested for hemagglutinating activity with chicken red-blood cells following standard methods (Swayne et al. 1998). We extracted RNA from VAF harvested from all dead embryos and the hemagglutinating VAF from live embryos using the MagMAX-96 Viral Isolation Kit (Ambion Inc., Austin, Tex.). RNA was tested for AIV with a 1-step rRT-PCR targeting the matrix gene (Spackman et al. 2003). We defined positive samples as those that were PCR positive (0-35 C_T) after demonstrating hemagglutinating activity. We performed genetic subtyping by characterizing the hemagglutinin (HA) and neuraminidase (NA) gene using rRT-PCR, with universal primers (Hoffman et al. 2001, Phipps et al. 2004). We purified amplicons with cleanup columns (Millipore, Bedford, Mass.) and submitted them for sequencing. We aligned sequences (Invitrogen VectorNTI), then compared them with previously described isolates in the NCBI (<http://www.ncbi.nlm.nih.gov/blast/Blast.cgi>) to determine subtype.

Results

Crow movements and WNV infections

We recorded 4,446 locations from the radio-marked crows between February and October 2005, of which 3,363 locations were used for our movement analyses. The crows used 6 roost sites regularly within the Davis city limits (Figure 1A). Crows moved frequently between roost sites using a mean of 1.7 roosts in July to a mean of 3.6 roosts in June (Figure 2A). The use of roost sites increased from February to June, followed by a decline in the number of roost sites from July to October. The mean distance traveled daily between roost and feeding sites ranged from 2,016 m in June to 3,934 m in August (Figure 3A). The mean distance traveled between roost sites ranged from 120 m in July to 492 m in April.

At the time of capture, 54 of 55 marked crows were EIA-WNV negative, with the exception of 1 crow that tested positive for Western equine encephalitis virus (WEEV). During the same months, no WNV positives (EIA-PRNT) were found in crows captured for surveillance. As the study progressed, 50 of the radio-marked crows were lost to monitoring, and 5 crow carcasses were recovered, all of which were necropsied.

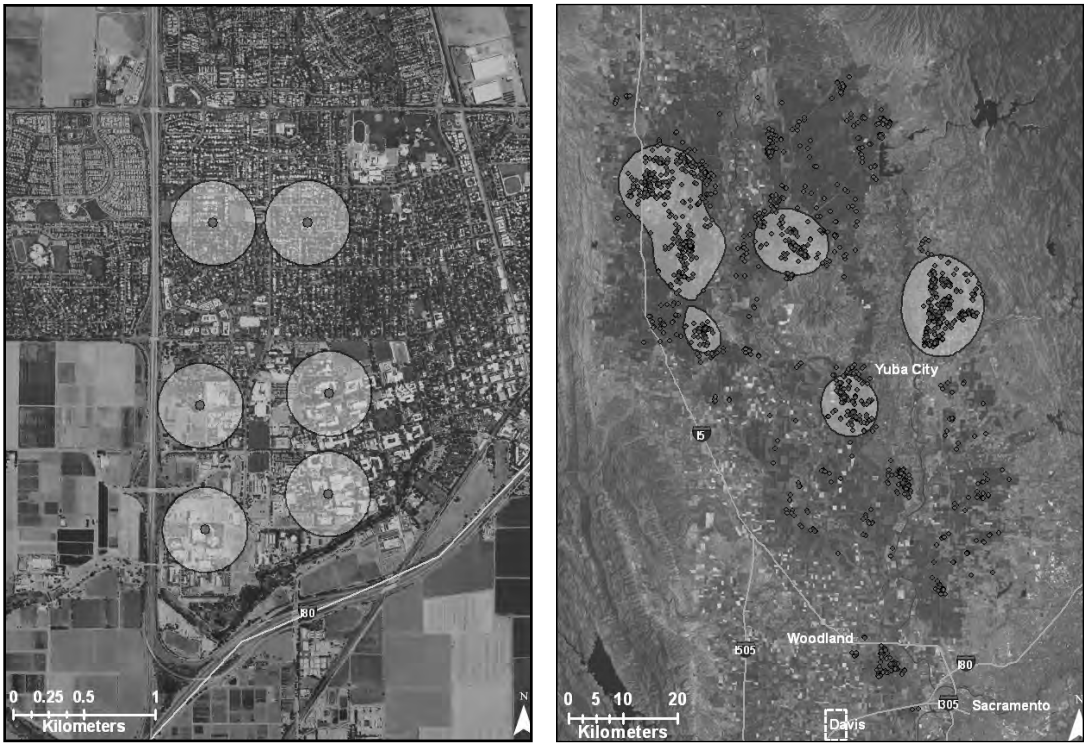

Figure 1. (**A**) The relative size of roost distribution of American crows within University of California–Davis campus showing individual roosts (dots) surrounded by a 300m buffer. (**B**) Roost distribution of greater white-fronted geese within the Sacramento Valley with individual roosts and zones of roosting (circles) based on 65% fixed-kernel contour analyses.

Table 1. Monthly habitat use by greater white-fronted geese in the Sacramento Valley during 1998–2000. Habitat use is based on the number of telemetry locations recorded at each habitat type divided by the total number of locations recorded (*n*; after Ackerman et al., 2006).

		Habitat type							
Month	*n*	Barren	Grass	Non-rice agriculture*	Open water	Perma-nently flooded wetland	Rice	Seasonally flooded wetland	Wetland
November	897	3.5%	7.3%	5.0%	0.1%	2.1%	52.7%	21.6%	7.7%
December	1215	5.2%	5.7%	12.3%	0.4%	3.1%	49.7%	17.9%	5.8%
January	1150	9.2%	5.7%	18.7%	1.3%	1.7%	49.6%	11.2%	2.7%
February	1019	9.4%	5.8%	24.1%	1.7%	3.3%	39.2%	14.0%	2.5%
March	182	6.6%	7.7%	41.8%	2.8%	2.2%	19.2%	17.0%	2.8%
Total	4463	6.9%	6.1%	16.4%	1.0%	2.6%	46.6%	16.0%	4.5%

* Non-rice agriculture includes wheat, corn, milo, onion, sunflower, black dirt, fallow bare and fallow weeds

Two of the 5 crow carcasses were RT-PCR WNV positive (40% minimum mortality rate).

Goose movements and AIV

Overwintering geese moved much greater distances than did crows (Figures 1B and 3B). The mean distance traveled daily between roosting areas and feeding sites ranged from 1.9 km in March to 13.2 km in November. The mean distance traveled between different

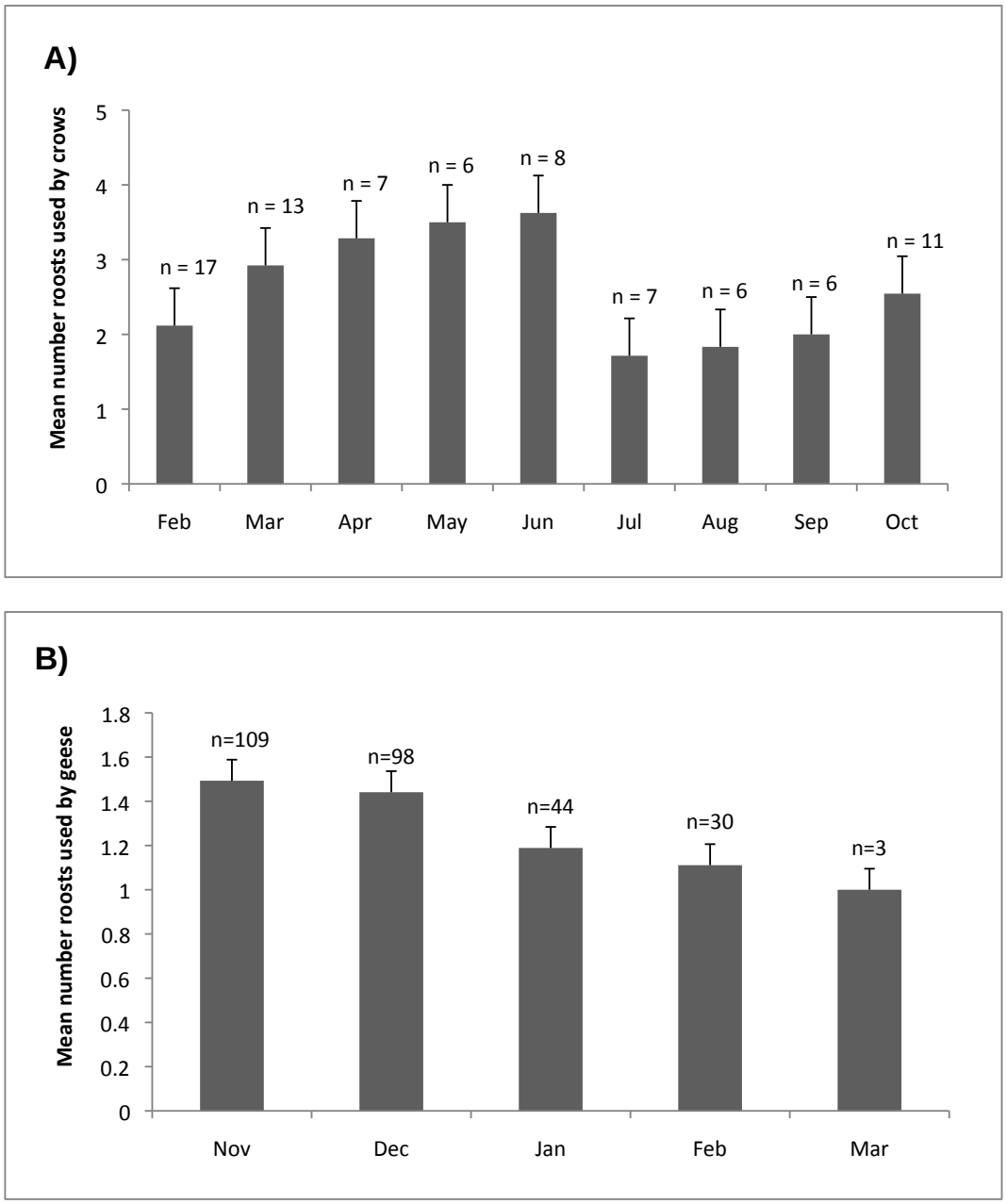

Figure 2. The mean number of roosts used each month (with standard errors) for (**A**) American crows within the University of California–Davis campus, and (**B**) greater white-fronted geese in the Sacramento Valley. The number of birds included in the analysis for each month is shown above error bars.

roosting areas ranged from 4.2 km in March to 19.3 km in January. Geese exhibited greater roost fidelity than crows, occupying a mean of 1.0 roosting zones in March and 1.5 roosting zones in November (Figure 2B). Geese spent most of their time during the day in rice fields (Table 1) during November (52.7%), December (49.7%), January (49.6%) and February (39.2%), although in March, they were commonly found in nonrice agricultural fields (41.8%). The second most commonly used habitat type was seasonally flooded wetlands (mean = 16.0%). The geese spent <10% of their time in barren areas, grass, open water, or wetland habitats.

The overall prevalence of AIV in the goose population during 2007 to 2009 was 3.2%

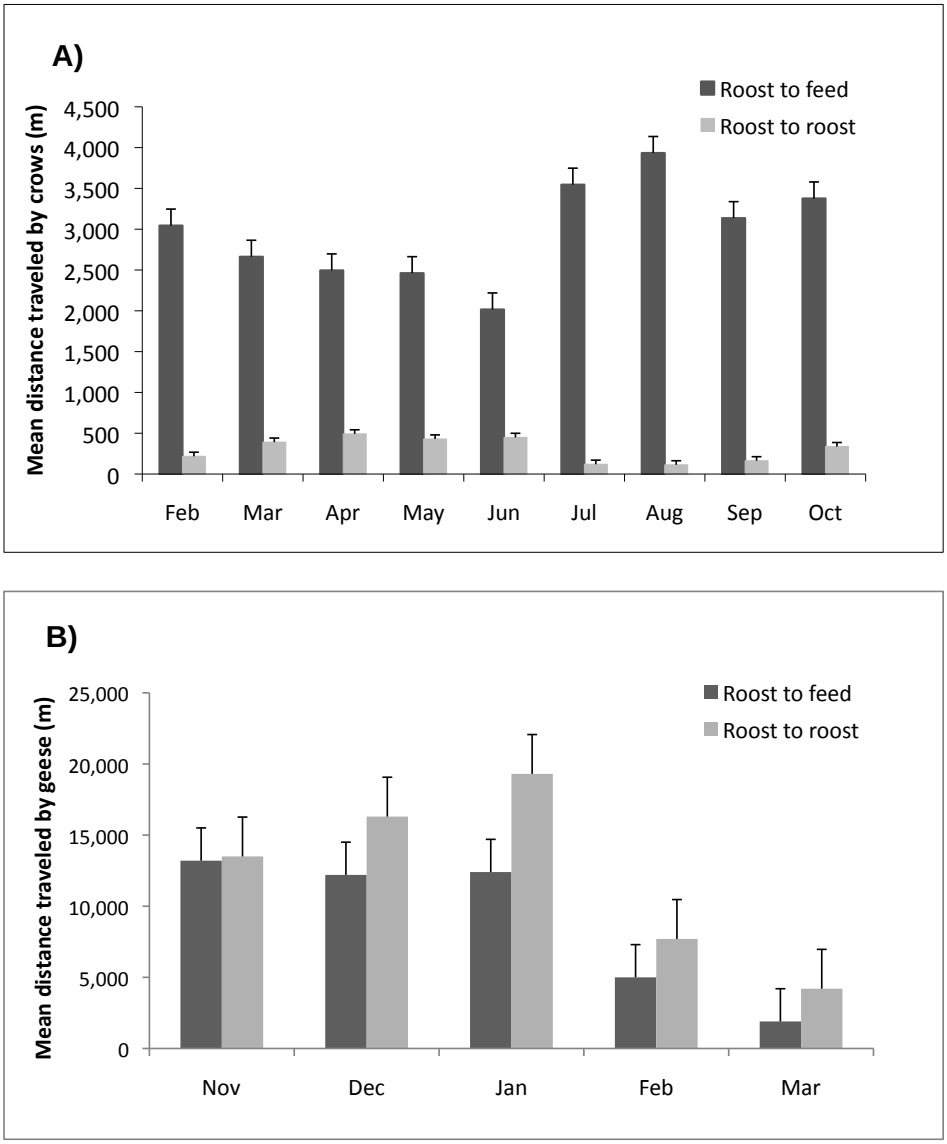

Figure 3. Mean distances traveled each month (with standard errors) between roost-to-feed and roost-to-roost sites by (**A**) American crows at the University of California–Davis campus; and (**B**) greater white-fronted geese at the Sacramento Valley.

(6/187). All positives were detected during the early wintering period from late October to mid-December. Three subtypes of AIV (H6N1, H1N1 and H10N7) were isolated; all of which were low pathogenic subtypes. The prevalence of H6N1 was 2.14% (4/187), while the other 2 subtypes were found in single individuals (1/187, prevalence of 0.53% each).

Discussion

Spatial aggregation and movement patterns of birds are a key factor in understanding a number of disease systems (Clayton and Moore 1997, Takekawa et al. 2010, Altizer et al. 2011). In the case of arthropod-borne pathogens, synchronization of bird aggregation and movement with vector abundance helps define disease dynamics (Clayton and Moore 1997, Kramer et al. 2008). We determined that American crow movements between roosting and foraging areas were concentrated within an area of a few kilometers. In contrast, movements of greater white-fronted geese encompassed most of the Sacramento Valley.

The vastly different roosting and feeding habits of these species affords insights into how each could aid in the maintenance and spread of pathogens. Key to the persistence and spread of diseases is the concept of the disease focus or nidus (reviewed by Boyce et al. 2009). Each disease has its own distribution or focus that is temporally and spatially variable. Host diversity, vector diversity (in case of vector-borne diseases), and environmental factors help to determine the limits and variability of the foci. In the following sections, we discuss both of the systems in relation to the foci of disease.

Roosting behavior of crows and WNV transmission

The transmission of WNV depends on the distribution of mosquito vectors (primarily *Culex* spp.), biting rates, host preference, roosting behavior, and contact rates among hosts (Sardelis et al. 2001, Kilpatrick et al. 2005, Reisen et al. 2006, Kramer et al. 2008, Nielsen et al. 2008, Diuk-Wasser et al. 2010). Studies also show roost size and summer temperatures to be important factors affecting WNV activity (Nielsen et al. 2008, Diuk-Wasser et al. 2010). American crows are highly competent hosts (Brault et al. 2004) that are likely to help in the amplification of WNV, whereas other passerines contribute toward persistence and spread of WNV (Reisen et al. 2006, Kwan et al. 2010). Since its arrival in North America, WNV spread from its original focus in New York state on a westward direction across the continent with a slower progression along a north-south direction (Komar et al. 2003, Kramer et al. 2008). This suggests a greater involvement of local bird movements, rather than north-south migration movements (Rappole et al. 2006). Also, diverse vector-competent mosquito species aided in bridging emerging local virus foci, resulting in the unprecedented spread of WNV.

Because WNV causes morbidity and mortality in many bird species, infections could affect normal movement patterns in susceptible species (e.g., Ward et al. 2006). Most crows in our study disappeared before the expected battery life of the radio tags had expired. Their disappearance could be attributed to dispersal or mortality of crows outside of the study area. Crows moved among roosting sites, although the average distances traveled was low. Mean distances traveled by crows between roosting sites was between 113 and 492 m/month, whereas crows in Illinois traveled about 1,038 m/day (Ward et al. 2006). A decline in the mean number of roosts used per month and the movement between roosts during July to September was observed in both years. Concomitantly, an increase in movements between roost and feeding sites occurred during the same months, suggesting that lower food availability may have forced crows to fly greater distances in search of food. Although crows infected with WNV tend to become more active 5 days prior to death in some sites (e.g., Illinois; Ward et al. 2006), this is not the case in California, where infected crows may die within 1 day of infection (Nielsen and Reisen 2007).

WNV activity in CCV tended to be the highest between July and September (Elnaien et al. 2006, Nielsen et al. 2008, Reisen et al. 2009) when temperature patterns are optimum for several *Culex* vector species (Barker et al. 2010). Nielsen et al. (2008) showed that *C. pipiens* and *C. tarsalis* populations in Davis have distinct spatial and temporal distribution patterns that affect WNV activity. Thus, mosquito feeding patterns and the movement and distribution of birds in roosting sites influenced WNV activity (Reisen et al. 2004, Nielsen and Reisen 2007, Nielsen et al. 2008). Also, Western scrub jays (*Aphelocoma californica*), house finches (*Carpodacus mexicanus*), house sparrows (*Passer domesticus*), northern cardinals (*Cardinalis cardinalis*), and American robins are competent hosts and are likely important dispersers of WNV (Reisen et al. 2005, Ward et al. 2006, Kilpatrick et al. 2007, Nielsen et al. 2008). Movement patterns of each of these species vary significantly, and their involvement in WNV epidemiology vary with their density and dispersal patterns. However, a recent study suggests that WNV is unlikely to disperse long distance via bird movements. Although WNV transmission has been detected repeatedly on mainland California since 2003, Boyce et al. (2011) found no evidence that previously infected birds had flown the 30 km distance from the mainland to Santa Cruz Island. In that study, WNV antibodies were not detected among 25 species of migrating birds sampled on the island in 2007 and 2008. Similarly, serological studies involving 43 species of neotropical migrants could not find

evidence of WNV entering California with south-north migrating birds (Reisen et al. 2010).

Movements of greater white-fronted geese and avian influenza transmission

Greater white-fronted geese typically used <2 roosting sites per month, although they traveled large distances between roosts and between roosts and feeding areas. Roost-to-roost movements were similar to roost-to-feeding area movements in November, but, from December through February, roost-to-roost movements became successively greater (Figure 2B; Table 1). Roost-to-feeding-site movements reflected availability of food, and, with the progressing winter, food became increasingly concentrated, reducing their need to fly great distances. Local resource depletion likely causes an increase in the distances traveled between roost and feeding sites in several species and subspecies, including Tule greater white-fronted geese (*Anser albifrons elgasi*; Hobbs 1999), Canada geese (*Branta Canadensis*; Austin 1989), and greater snow geese (*Chen caerulescens atlantica*; Hill and Frederick 1997). Thus, as winter progressed, each of the species foraged over greater distances to acquire food.

Avian influenza virus foci are limited to areas that waterbirds used, including agricultural lands, wetlands, or other water bodies. Although collection of AIV samples was temporally separated from the spatial movement studies, the prevalence of AIVs served as a proxy to help understand AIV spreading patterns in relation to movement. Sampling of AIV was conducted between October and December, and most of the positive samples were detected from birds harvested in November, with the exception of a single bird being sampled in December. Avian influenza virus subtypes collected from Eurasia indicate clear peaks in the prevalence of AIVs in greater white-fronted geese, with near-zero prevalence before and after these peaks (Kleijn et al. 2010). We did not detect any such peak, although in North America it is generally observed that migrating birds arriving at their wintering grounds have low prevalence of AIVs that continue to decline as the winter progresses (Webster et al. 1992, Kraus et al. 2004).

The movement pattern of the greater white-fronted geese indicates that geese could help spread AIV between roosting and feeding areas. Ducks in these same habitats also play an important role due to their higher susceptibility and reservoir potential (Webster et al. 1992, Kraus et al. 2004, Munster et al. 2007, Hill et al. 2010). Mallards (*Anas platyrhynchos),* northern pintails (*Anas acuta*), northern shovelers (*Anas clypeata*), and other ducks are present in the CCV in large numbers during the winter. These species are susceptible to AIV infections, and high prevalences have been reported throughout their distribution (Kraus et al. 2004, Munster et al. 2007, Hill et al. 2010), aiding in the perpetuation of AIVs during the winter (Webster et al. 1992). Other species, such as Canada geese, that have significant urbanized populations typically have low prevalence of AIVs (Harris et al. 2010). Although Canada geese have been implicated in AIV perpetuation (Pasick et al. 2007), their low prevalence and the limited persistence of AIV in their feces suggest that they are of less importance in AIV epidemiology in North America (Harris et al. 2010).

Central to the perpetuation of AIVs is their ability to persist in water (Stallknecht et al. 1990, Brown et al. 2007, van Gils et al. 2007, Latorre-Margalef et al. 2009, Lebarbenchon et al. 2009, reviewed in Takekawa et al. 2010). Mallards experience a reduction in viral shedding rates as the season progresses due to acquired transient immunity, making mallards unsuitable for long-distance dispersal of AIVs at the end of the season (Latorre-Margalef et al. 2009). The greater distances that greater white-fronted geese move initially between roosts and feeding areas (October, November) could help to spread AIVs over a relatively large wintering area. The decline in such movements with increased food availability and decreased shedding rates (if similar transient immunity occurs in greater white-fronted geese) could reduce AIV prevalence in geese and limit AIVs to smaller foci during the period of north to south arrival. The arrival times of other duck species and their immunological state during this latter part of winter could, then, become more important, helping to perpetuate infections until birds are ready for their northward migration in the spring (Webster et al. 1992, Olsen et al. 2006).

Changes in the CCV in the 1990s have resulted in concomitant changes in goose distribution and habitat use, with a marked reduction in

the size of home ranges and distances travelled between roosts and feeding areas (Ackerman et al. 2006). This has mainly been due to availability of food within relatively smaller areas, resulting in a more concentrated distribution of geese that move shorter distances to acquire food. Reduction of distances traveled by greater white-fronted geese in our study could also have been the result of infections. Infected Bewick's swans (*Cygnus columbianus bewickii*) showed significantly lower foraging rates, reduced foraging distances, and delayed departure dates from their wintering areas (van Gils et al. 2007), suggesting that AIVs in the wild could have more clinically and ecologically significant effects on waterfowl than previously suspected.

Movement ecology and virus transmission

The internal physiological state of birds and their capacity to move determine the extent of movements (Nathan et al. 2008), and are both influenced by seasonality and disease, among other factors (Reisen et al. 2006, Ward et al. 2006). Mosquito vectors are important in maintaining WNV among hosts, even when those hosts are relatively widely distributed (Reisen et al. 2004, 2006, Wheeler et al. 2009). The presence of dense American crow populations with spatially clustered roosts permits amplification of the virus in and around these roosts that is then spread to other hosts, including humans, by competent vectors (Reisen et al. 2006, Wheeler et al. 2009). Local movement patterns of American crows and other passerines may aid in the distributional changes of WNV. Spatial and temporal patterns of mosquito distribution, diversity of competent mosquito vectors, diversity of host distribution and movement patterns, habitat characteristics, and temperature variation have permitted WNV, unlike AIVs, to spread over very heterogeneous landscapes.

Waterbirds are limited to aquatic or semi-aquatic habitats, and opportunities to assemble different species are temporally and spatially limited. Ducks and geese infected with AIVs respond differently relative to different subtypes of AIV (Swayne 2008). Mild disease is commonly reported for LPAI virus-infected ducks and geese, especially juveniles, and limited studies documented that even LPAI viruses may influence departure dates from staging areas, as well as distances traveled (van Gils et al. 2007, Latorre-Margalef et al. 2009, Lebarbenchon et al. 2009, Jourdain et al. 2010). Because wetlands are staging areas and migratory pathways where ducks and geese congregate are spatially limited, AIVs circulate only in association with such areas, with spillover occurring in interfaces with domestic and wild birds (such as in southern and eastern Asia). Bird movements strongly affect these interfaces, and unraveling the various interacting factors influencing movement in birds constitutes a significant challenge in our understanding of movement and AIV ecology.

Bird movements play an important role in the perpetuation, expansion, and evolution of viruses, although they are not quantified at the level necessary. Quantifying the movement of infected and uninfected birds could help determine how disease influences movement. Controlled laboratory experiments in combination with selected field experiments may be key for improving our knowledge of movement and disease ecology. Satellite telemetry already has served as an important tool in understanding movement patterns in relation to the spatial and temporal distribution of disease foci (Boyce et al. 2009, Takekawa et al. 2010). Our results highlight the importance of bird movements in the likely local movement, maintenance, and spread of 2 important viruses in California. Gaps in our understanding of the movement ecology of bird species involved in the epidemiology of viruses needs to be better understood through further studies, targeting key species known to be competent hosts for WNV and AIVs.

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