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West Nile Virus and California Breeding Bird Declines

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Abstract: Since it was first detected in 1999, West Nile virus (WNV) quickly spread, becoming the dominant vector-borne disease in North America. Sometimes fatal to humans, WNV is even more widespread among birds, with hundreds of species known to be susceptible to WNV infection in North America alone. However, despite considerable mortality and local declines observed in American crows *(Corvus brachyrhynchos)*, there has been little evidence of a large regional association between WNV susceptibility and population declines of any species. Here we demonstrate a correlation between susceptibility to WNV measured by large-scale testing of dead birds and two indices of overall population change among bird species following the spread of WNV throughout California. This result was due primarily to declines in four species of Corvidae, including all species in this family except common ravens *(Corvus corax)*. Our results support the hypothesis that susceptibility to WNV may have negative population consequences to most corvids on regional levels. They also provide confirmation that dead animal surveillance programs can provide important data indicating populations most likely to suffer detrimental impacts due to WNV.

Keywords: avian populations, Breeding Bird Survey, Corvidae, vector-borne disease

Introduction

West Nile virus (WNV) is an invasive mosquito-borne disease that quickly spread throughout North America after it was first detected in New York City in 1999 (Lanciotti et al., 1999; Hayes and Gubler, 2006). As of December 11, 2006, WNV has been responsible for over 23,000 human cases and 931 fatalities in the U.S. (CDC, 2006), making it the dominant vector-borne disease on the continent (Kilpatrick et al., 2006).

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Debilitating and sometimes fatal in humans, WNV affects a wide taxonomic range of species, from alligators to horses (Komar, 2003; Klenk et al., 2004). The disease is particularly devastating to wild birds, with over 200 native species known to suffer morbidity and mortality attributable to WNV infection in North America (CDC, 2006). Especially vulnerable to WNV are crows, jays, and magpies (family Corvidae) (Komar, 2003; Komar et al., 2003). Of this group, American crows are common, widespread, and particularly susceptible to the strain of WNV introduced in North America (Brault et al., 2005), and several studies have indicated that mortality in this species due to WNV can be dramatic. Hochachka et al. (2004), for example, analyzed Christmas Bird Count data and found strong local declines in American crows related to WNV in several sites in the northeastern U.S. Based on marked individuals, Yaremych et al. (2004) found a mortality rate of 68% due to WNV in 28 American crows in east-central Illinois, while Caffrey et al. (2003, 2005) documented the loss of 65% of individuals within a population in Oklahoma during a single season of WNV exposure. Despite these findings, studies at larger geographic scales have failed to detect unambiguous evidence of regional declines attributable to WNV in American crows or other susceptible species (Bonter and Hochachka, 2003; Caffrey et al., 2003; Marra et al., 2004).

In California, WNV was first isolated in 2003 from mosquitoes in three southern California wetlands (Reisen et al., 2004). It became widespread throughout the state in summer of 2004, when 830 human cases were reported and 3,232 dead birds tested positive (CDHS, 2006). Thus, although some local effects may have been expressed earlier, WNV is likely to have had widespread impacts on the state's avian populations for the first time between summer 2004 and the 2005 spring breeding season. This rapid geographic expansion provides a sharp temporal divide contrasting with the situation examined in previous studies (e.g., Hochachka et al., 2004) and offers an excellent opportunity to detect the effects of WNV on a large geographic scale.

Our goal here is to investigate the hypothesis that WNV significantly affected avian populations in California by comparing data on prevalence of WNV from dead birds collected throughout the state with survey data on breeding birds. In contrast to prior studies, our analysis is interspecific and includes data from 29 species of birds for which sufficient data on WNV prevalence in California were available. Data on population changes were tested for relationships with WNV prevalence and the migratory status of the species under the assumption that resident species are likely to have experienced greater exposure to the disease than migrants. Given the known susceptibility of corvids to WNV, we predicted a priori that species in this family should exhibit relatively strong population declines.

Materials and Methods

As indices of avian population size in California, we used changes in numbers of birds counted between successive breeding seasons by the North American Breeding Bird Survey (BBS). BBS, organized by the USGS Patuxent Wildlife Research Center, are conducted at the height of the breeding season at localities throughout North America and consist of counting all birds seen or heard during 3-minute point counts at 50 stops, 0.8 km apart. Prior studies have demonstrated considerable variation attributable to the person performing the survey (Sauer and Peterjohn, 1994). Thus, we used only surveys that were conducted by the same individual in the 2 years being compared. Further details are available at http://www.pwrc.usgs.gov/BBS.

We examined all surveys conducted throughout California from 1994–1995 to 2004–2005 ($x = 74$ year^{-1}, range = 65–88). Maps of BBS routes are available at http://www.nationalatlas.gov/natlas/Natlasstart.asp; relevant here is that routes are relatively evenly distributed throughout the state. Two measures were used to estimate population changes from one year to the next. First, we calculated the percent of surveys exhibiting a decline between each pair of successive years ("% decline"). This value provides a statewide index of the probability of declines having been suffered by each species. Second, we estimated the overall magnitude of annual changes by calculating the difference between the numbers of each species counted in each survey between successive years. The absolute value of this number was then log-transformed (log[|difference in number of birds counted|+1]) in order to help equalize variances and normalize the data (e.g., Koenig and Liebhold, 2005) and the sign changed to indicate an increase (+) or decrease (−) from year x to year $x+1$. Log-transformed values were then averaged across all sites to yield a statewide index of the overall change in population size for the species between the 2 years ("mean change").

We assumed a priori that values from 2004–2005, the first year that WNV was present throughout the state, encompassed the major effects of the disease. Values from the prior 10 sets of years, during which time the disease was either absent or not widespread within the state, were considered controls.

To relate these statewide population effects to WNV, we would ideally want to know both the rates of exposure and the susceptibility of infected individuals during the period of interest. Unfortunately, exposure rates are unknown. Furthermore, the number and diversity of non-corvid species tested in 2004 was low, making use of data from 2004 alone a poor index of WNV prevalence for most species. Thus, we assumed exposure to be equivalent across species and used prevalence data based on all dead birds tested by the California Department of Health Services (CDHS) during 2004 and 2005 combined as an index of susceptibility.

Testing was performed as follows. In 2004 and 2005, CDHS, through the California Dead Bird Surveillance Program, coordinated the testing of over 13,000 dead birds reported to the California West Nile Virus Hotline (Hom et al., 2005). Although more than 100 species tested positive for WNV, we restricted our analyses to the 29 species of passerines for which at least 20 individuals were tested.

Dead birds collected in regions with no local agency testing were sent to the California Animal Health and Food Safety Laboratory (CAHFS) for necropsy and the Center for Vectorborne Diseases (CVEC) for detection of viral DNA via real-time polymerase chain reaction (RT-PCR) (Kauffman et al., 2003). WNV testing at the local agency level was limited to corvids. Rapid assays included the VecTest™ (Medical Analysis Systems, Camarillo, CA), a rapid antigen-capture wicking assay, or the Rapid Analyte Measurement Platform (RAMP, Response Biomedical Corporation, Burnaby, BC, Canada), both of which have high sensitivity to WNV, particularly in corvids (Stone et al., 2005). American crows testing positive by rapid assays were not confirmed by further testing.

All negative WNV results from rapid assays were confirmed to prevent false negatives. Species besides American crows testing negative for WNV using rapid assays were sent to CAHFS for necropsy and CVEC for RT-PCR confirmation. Rapid assay buffer from crows testing negative for WNV were confirmed via RT-PCR at CVEC or participating local public health laboratories.

Migratory status was based on the primary mode exhibited by birds of each species within the state based on Grinnell and Miller (1944). White-crowned sparrows *(Zonotrichia leucophyrs)*, for example, were classified as primarily migratory, even though a resident race inhabits coastal California. Results did not change if these intermediate species were considered residents. Table 1 provides a list of species examined and a summary of the data.

Values for WNV prevalence and percent BBS routes declining were arcsin-transformed for analysis. *P*-values are two-tailed.

Results

Among the 29 species of passerines for which at least 20 individuals were tested, prevalence of WNV varied from 3.8% to 81.5%. Between 2004 and 2005, declines and mean population change among the species considered were significantly correlated with WNV prevalence, using both all species and primarily resident species only (Table 2). Specifically, species with high WNV prevalence experienced a greater proportion of sites declining and were more likely to have suffered a population decline between these 2 years. No significant relationship between these variables was found using the 10 migratory species only (Table 2).

Examination of the data (Fig. 1) indicates that these correlations were largely due to four of the five species of corvids analyzed (American crow, yellow-billed magpie *Pica nuttalli*, Western scrub-jay *Aphelocoma californica*, and Steller's jay *Cyanocitta stelleri*). These species, all residents, exhibited both significantly higher prevalence values (Mann–Whitney *U*-tests; $z = 2.53$, $P = 0.008$ [vs. all other species], $z = 2.40$, $P = 0.014$ [vs. other residents only]) and greater population declines between 2004 and 2005 by either measure than both all other species and resident species (four Mann–Whitney *U*-tests; all $z \geq 2.3$, all $P \leq 0.018$).

In contrast, there was no significant relationship between WNV prevalence and the two measures of population change among either all species or among resident species only in any of the 10 pairs of successive years between 1994–1995 and 2003–2004, before WNV became widespread in the state (Table 2). There was also no tendency for the four species of corvids with high WNV prevalence to exhibit greater declines compared to the other species during any of the other 10 pairs of years prior to 2004–2005 by either measure of population change (20 Mann–Whitney *U*-tests; all $z \leq 1.3$, all $P \geq 0.19$). Among the primarily migratory species, the only analyses yielding significant correlations were those between WNV prevalence and declines observed between 2003–2004 (Table 2).

Given the large number of analyses performed, it is likely that some tests will yield significant results by chance. However, the probability that the establishment of WNV between 2004–2005 would adversely affect populations of susceptible species, and particularly of resident susceptible species, between 2004–2005 only can be approximated using Fisher exact tests. Specifically, the chances of observing 2 of 2 significant results during the target year (2004–2005) and 0 of 20 significant results for other years (1994–1995 through 2003–2004), as found for both all species and resident species only (Table 2), is $P = 0.004$. In contrast, the results for migratory species (0 of 2 significant results during the target year and 2 of 20 significant results for non-target years) is $P = 0.82$.

Measured by the percent of BBS routes declining, 2004–2005 was the worst of the 11 years examined for both American crows (2004–2005: 68.6%; $x \pm$ SD of other 10 years = 44.9 ± 11.1%, range 32.5–67.6%) and yellow-billed

Table 1. Species and Data Used in the Analyses

Species	Scientific name	*N* birds tested	% WNV prevalence	Primarily resident?	Change from 2004–2005	
					% Routes declining	Mean change[a]
Black phoebe	*Sayornis nigricans*	45	17.8	Yes	51.3	−0.240
Yellow-billed magpie	*Pica nuttalli*	818	81.5	Yes	60.0	−1.007
Steller's jay	*Cyanocitta stelleri*	184	48.9	Yes	51.2	−0.171
Western scrub-jay	*Aphelocoma californica*	2,062	69.8	Yes	57.7	−0.492
Common raven	*Corvus corax*	336	13.7	Yes	38.5	0.183
American crow	*Corvus brachyrhynchos*	5,294	56.4	Yes	68.6	−0.650
European starling	*Sturnus vulgaris*	245	9.0	Yes	41.8	0.161
Red-winged blackbird	*Agelaius phoeniceus*	42	7.1	Yes	44.2	−0.130
Brewer's blackbird	*Euphagus cyanocephalus*	209	13.9	Yes	49.1	0.064
Purple finch	*Carpodacus purpureus*	24	8.3	Yes	30.6	0.235
House finch	*Carpodacus mexicanus*	646	23.2	Yes	64.2	−0.841
American goldfinch	*Carduelis tristis*	54	9.3	Yes	56.3	0.023
Lesser goldfinch	*Carduelis psaltria*	144	25.0	Yes	51.0	−0.337
Pine siskin	*Carduelis pinus*	112	11.6	No	47.1	−0.135
White-crowned sparrow	*Zonotrichia leucophrys*	105	3.8	No	50.0	−0.120
Dark-eyed junco	*Junco hyemalis*	62	6.5	No	60.5	−0.541
Song sparrow	*Melospiza melodia*	32	9.4	Yes	31.3	0.133
Fox sparrow	*Passerella iliaca*	70	20.0	No	43.8	0.042
Spotted towhee	*Pipilo maculatus*	32	21.9	Yes	41.1	0.262
California towhee	*Pipilo crissalis*	103	14.6	Yes	35.7	0.213
Black-headed grosbeak	*Pheucticus melanocephalus*	52	21.2	No	36.4	0.246
Western tanager	*Piranga ludoviciana*	47	29.8	No	50.0	−0.053
Barn swallow	*Hirundo rustica*	20	20.0	No	34.2	0.309
House sparrow	*Passer domesticus*	633	13.4	Yes	52.3	−0.100
Northern mockingbird	*Mimus polyglottos*	161	19.3	Yes	48.6	0.022
Swainson's thrush	*Catharus ustulatus*	53	13.2	No	54.6	−0.452
Hermit thrush	*Catharus guttatus*	120	5.8	No	40.9	−0.030
American robin	*Turdus migratorius*	200	26.0	No	46.6	−0.142
Western bluebird	*Sialia mexicana*	51	43.1	Yes	30.2	0.444

[a]Mean log-transformed difference between the absolute value of counts, with positive values indicating an increase and negative values a decrease (see text).

magpies (2004–2005: 60.0%; $x \pm$ SD of other 10 years = 47.5 ± 8.2%, range 31.3–57.1%). The 2004–2005 declines were the third worst for the Western scrub-jay and the fifth worst for the Steller's jay. Based on mean population changes, 2004–2005 was the worst year for yellow-billed magpies (2004–2005: −1.007; $x \pm$ SD of other 10 years = 0.041 ± 0.282, range –0.423 to 0.562), the second worst for the American crow and Western scrub-jay, and the fifth worst for the Steller's jay. Ranking the years from the best (lowest percent of BBS routes declining or greatest mean population change) to worst, and summing ranks of these four species, the 2004–2005 decline was the worst observed out of the 11 pairs of years for these taxa (% decline: 2004–2005 sum of ranks = 38, $x \pm$ SD sum of ranks for other pairs of years = 22.6 ± 5.4, range 15–28; mean change: 2004–2005 sum of ranks = 38, $x \pm$ SD sum of ranks for other pairs of years = 22.6 ± 6.6, range 13–35).

Discussion

In contrast to prior analyses, our results indicate that WNV, a vector-borne disease that has recently invaded and spread throughout North America, has had significant negative impacts on avian populations at a large geographic scale. Correlations between WNV prevalence and both the

Table 2. Pearson Correlations between the Percent WNV Prevalence Based on the 2004–2005 CDHS Survey and Two Measures of Population Changes in California Birds Based on Breeding Bird Surveys Conducted between 1994 and 2004[a]

Years	All species (N = 29)		Resident species only (N = 19)		Migratory species only (N = 10)	
	% Decline	Mean change	% Decline	Mean change	% Decline	Mean change
Prior to establishment of WNV						
1994–1995	0.05	−0.11	0.16	−0.24	−0.20	0.23
1995–1996	0.03	−0.06	−0.25	0.28	0.35	−0.43
1996–1997	0.22	−0.15	0.20	−0.13	0.19	−0.06
1997–1998	0.27	−0.15	0.16	−0.04	0.55	−0.42
1998–1999	−0.31	0.30	−0.41	0.32	−0.05	0.19
1999–2000	−0.17	0.30	−0.11	0.30	−0.44	0.43
2000–2001	0.19	−0.18	0.19	−0.19	0.40	−0.29
2001–2002	−0.18	0.16	−0.07	0.14	−0.41	0.25
2002–2003	0.00	0.02	0.01	−0.03	0.13	0.38
2003–2004	0.10	0.04	−0.12	0.22	0.69*	−0.64*
Following establishment of WNV						
2004–2005	0.37*	−0.46*	0.50*	−0.63**	−0.34	0.43

[a]% Decline, percent BBS routes exhibiting a decline between the 2 years; Mean change, mean log-transformed difference between the absolute value of counts, with positive values indicating an increase and negative values indicating a decrease (see text).
*$P < 0.05$; **$P < 0.01$ (two-tailed); other $P > 0.05$.

proportion of sites within California exhibiting a decline and the mean change in count numbers were significant for all species and for resident species only between surveys conducted in 2004–2005, immediately following the spread of WNV throughout the state. No comparable declines were observed among these two groups of species for any of the prior 10 pairs of years, during which time WNV was either absent or restricted within the state. These are significant results, as the probability of observing such patterns by chance given the a priori expectation of a relationship existing only after the widespread invasion of WNV in summer 2004 is small. Although other diseases may have confounded observed effects on some species such as the house finch *Carpodacus mexicanus* (see below), we can think of no alternative hypothesis that offers a plausible explanation for the significant relationship observed between population changes and apparent susceptibility to WNV coinciding with the invasion of this disease throughout the geographic area considered.

As expected from prior studies, population declines apparently related to WNV were particularly evident among members of the family Corvidae, including the two widespread species of jays and especially the American crow and yellow-billed magpie, among which the 2004–2005 decline was particularly strong. However, a fifth species of Corvidae, the common raven, suffered neither large declines nor high prevalence of WNV, suggesting that, in contrast to other species in this family, it is relatively unsusceptible to the disease. This species' relative immunity to WNV has apparently not been previously noted.

Most other species included in the analysis exhibited moderate prevalence of WNV and variable declines during the year WNV spread throughout the state. Two notable outliers were the Western bluebird *(Sialia mexicana)*, which exhibited relatively high WNV prevalence but no apparent decline between 2004–2005, and the house finch, which suffered a relatively high population decline between 2004–2005 but showed low WNV prevalence. Regarding the first of these species, Western bluebirds are apparently relatively unaffected by the disease despite exhibiting high prevalence, a finding clearly deserving of additional study. As for the latter species, house finches have been previously found to be competent potential reservoirs of WNV along with corvids (Komar et al., 2003), but are also susceptible to a variety of other diseases including avian pox (Zahn and Rothstein, 1999) and mycoplasmal conjunctivitis (Hochachka and Dhondt, 2000; Dhondt et al., 2006), both of which have been shown to affect populations of this species. Thus, the relatively large decline observed between 2004–2005 was possibly caused in part by factors other than WNV.

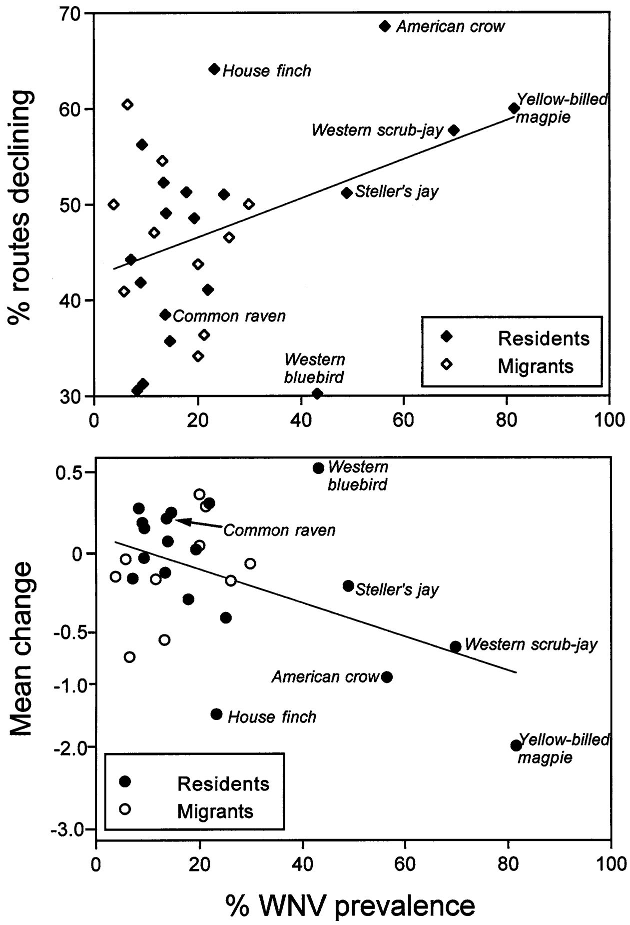

Figure 1. Relationship between the species-specific prevalence ([N positives/N birds tested] × 100, by species) of West Nile virus in dead birds analyzed in 2004 and 2005 by the California Department of Health Services divided between resident and migratory species, and two measures of mean population changes within California between 2004 and 2005 based on breeding bird surveys: the percentage of breeding bird survey routes for which numbers of that species declined (top), and the mean change in number of birds counted per route between 2004 and 2005 (bottom). The latter was calculated using log-transformed values with the sign changed to reflect increases (+) and decreases (-) between the 2 years (see text); values on the y-axis are back-transformed.

Of the pairs of years examined, only 2003–2004 yielded a significant correlation between WNV prevalence and BBS declines for the small number of primarily migratory species examined. This result is plausibly due to chance. Alternatively, WNV has been widespread in Mexico since summer 2002 (Estrada-Franco et al., 2003), and it is possible that this relationship reflects exposure of these species to the disease south of the U.S. border during the 2003 spring migration or the prior winter.

Our findings provide confirmation that dead bird surveillance programs, currently being conducted in numerous states throughout the U.S., provide information of significant value to understanding the vulnerability of different species to WNV. As such, they extend prior results by Hochachka et al. (2004), who found a strong relationship between numbers of dead American crows reported and WNV prevalence on a count-by-count level in New York State, as well as a relationship between numbers of dead crows reported and WNV prevalence measured in mosquito surveys. The data presented here support the conclusion that variation in WNV prevalence across species directly affects populations of those species on a large geographic scale, at least during the initial invasion phase of the disease.

The adverse effects of WNV on wildlife populations may clearly be significant, apparently inflicting at least temporary declines across populations that are related to the prevalence of the disease found among dead specimens. Improved and expanded efforts for reporting and testing dead birds are warranted, as are studies aimed at better integration of this and other emerging diseases with wildlife ecology.

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