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# Declines of Black-billed Magpie (*Pica hudsonia*) and Black-capped Chickadee (*Poecile atricapillus*) in the north-central United States following the invasion of West Nile virus

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Abstract.—West Nile virus (WNV) is an introduced pathogen, transmitted by mosquitos, that spread across North America following its arrival there in 1999. Birds host the virus, but consequences of the disease to bird species have been variable. A small number of avian species are especially susceptible to WNV, experience high mortality rates when infected, and have shown regional declines apparently because of the disease. Other species have seemingly been unaffected. Transmission of WNV is associated with climate, with higher incidence of transmission in dry areas with warm winters. The north-central United States is an area that exhibits clines in temperature and precipitation, and in this area changes in species abundance due to WNV have not been closely examined. We used Christmas Bird Count (CBC) data to investigate changes in winter abundance of selected species before and after the arrival of WNV in the Great Plains. After arrival of WNV, average estimated abundances of Black-billed Magpie (*Pica hudsonia*) were significantly lower than projected abundances across much of the Great Plains. Black-capped Chickadee (*Poecile atricapillus*) abundances reached their lowest counts in portions of the Great Plains immediately after the arrival of WNV and experienced overall negative annual declines from 1988 to 2017. Two other species that were examined did not experience changes in abundance across the study area. Abundances of Black-billed Magpies and Black-capped Chickadees have declined over the past 30 years in the Great Plains, and WNV has likely played a major role in recent declines of magpies throughout the study area.

Resumen.—El virus del Nilo Occidental (VNO) es un patógeno introducido transmitido por mosquitos que se diseminó por América del Norte luego de su llegada en 1999. Las aves albergan el virus, sin embrago, las consecuencias de la enfermedad para las especies de aves han sido variables. Hay un pequeño número de especies de aves que son especialmente susceptibles al VNO, éstas experimentan altas tasas de mortalidad cuando se infectan y han demostrado disminuciones en algunas regiones probablemente debido a la enfermedad mientras que otras especies aparentemente no se han visto afectadas. La transmisión del VNO está asociada con el clima, con una mayor incidencia de transmisión en áreas secas con inviernos cálidos. La parte central-norte de los Estados Unidos es un área que exhibe clinas en temperatura y precipitación, pero los cambios en la abundancia de especies debido al VNO no han sido examinados de cerca. Utilizamos datos del Conteo Navideño de Aves para investigar los cambios en la abundancia invernal de especies seleccionadas antes y después de la llegada del VNO a las Grandes Llanuras. Después de la llegada del VNO, la abundancia promedio estimada de la urraca del Hudson o (*Pica hudsonia*), fue significativamente menor que la abundancia proyectada en gran parte de las Grandes Llanuras. Las abundancias del carbonero de capucha negra (*Poecile atricapillus*) alcanzaron sus recuentos más bajos en porciones de las Grandes Llanuras inmediatamente después de la llegada del VNO y experimentaron disminuciones anuales negativas en general de 1988 a 2017. Otras dos especies examinadas no experimentaron cambios en las abundancias en el área de estudio. La abundancia de *Pica hudsonia* y *Poecile atricapillus* ha disminuido en los últimos 30 años en las Grandes Llanuras, y es probable que el VNO haya desempeñado un papel importante en los recientes descensos de urracas en toda el área de estudio.

Introduced pathogens can have devastating consequences on native wildlife (Atkinson et al. 1995, LaDeau et al. 2007). West Nile virus (WNV) is a mosquito-borne *Flavivirus* (Campbell et al. 2002) native to the Eastern Hemisphere. Birds are the principal host of WNV and the disease is transmitted by mosquitos, primarily those in the genus *Culex* (Campbell et al. 2002). WNV was introduced into eastern North America in 1999 (Campbell et al. 2002). By 2001, the virus had spread across North America (Campbell et al. 2002) as far west as Iowa (Rappole and Hubalek 2003). WNV spread throughout all of the central

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United States, reached California in 2002, and was found in the remainder of the United States in 2003 (Hayes et al. 2005, Gubler 2007).

More than 200 bird species native to North America are susceptible to WNV, and infected individuals typically suffer morbidity and mortality (Komar 2003, Komar et al. 2003). Population-level impacts to North American birds have been variable. The virus has caused declines in some species' populations while other species' populations have been largely unaffected (LeDeau et al. 2007). For example, several corvids (Corividae; crow, jays, and magpies) and certain grouse species are especially susceptible to WNV, experience high mortality rates when infected, and have shown regional declines apparently as a result of the disease (Komar et al. 2003, 2005, Caffrey et al. 2005, Conover and Roberts 2016, Stauffer et al. 2018). For some species, declines in abundance have been persistent and appear to be long-term (Foppa et al. 2011, George et al. 2015). Other species showed short-term population-level impacts following the appearance of WNV, but their populations have subsequently recovered (George et al. 2015).

Population-level effects on birds apparently caused by WNV not only vary by species but can also vary by region (Wheeler et al. 2009). This is possibly because climate and weather affect transmission of the disease. Increased WNV amplification and transmission are generally observed in regions that experience low precipitation and warm winters (Epstein 2001, Deichmeister and Telang 2011). The epicenter of WNV transmission to humans has been the western Great Plains (Gubler 2007), a region characterized by low average rainfall, low humidity, and warm summer temperatures, especially in southern areas (NOAA 2019). In Iowa, high WNV incidence in humans was associated with drier conditions (DeGroote et al. 2008). Unusually cool environmental temperatures in North Dakota reduced the WNV transmission season by nearly half compared to the preceding season (Bell et al. 2006). In Louisiana, increased wetland coverage was associated with a decrease in WNV prevalence (Ezenwa et al. 2007). Human outbreaks of WNV also have a relationship with precipitation during the previous year (Landesman et al. 2007).

WNV has been present in North America for more than 16 years, and numerous studies have evaluated changes in abundance of various avian species. However, studies have not evaluated whether there has been spatial variation in the changes in abundance of species in the north-central United States, and little work has evaluated impacts of WNV on vulnerable species specifically in the Great Plains. Given that climate patterns influence WNV incidence, we would expect that the magnitude of change in abundance of species vulnerable to WNV would be different over large geographic areas. Additionally, no other study has evaluated the impact of WNV on Black-billed Magpie (*Pica hudsonia*) abundance, despite dramatic declines in its breeding numbers over the last 2 decades in certain regions, especially central and western Nebraska (Mollhoff 2016, Silcock and Jorgensen 2018a).

Here, we evaluate changes in the abundance of 4 avian species in the north-central United States by using Christmas Bird Count data. Two of the species are known to be vulnerable to WNV, one species has shown moderate susceptibility to WNV, and one is not especially vulnerable to WNV. We predict declines in estimated winter abundances of vulnerable species from the years prior to WNV emergence (1988–2001) to after WNV (2003–2017). We predict that these declines will be greatest in regions that are dry and have warm winters, such as low-elevation areas in the West and the South. We also predict less pronounced declines in vulnerable species in colder and wetter regions, such as in the North and the East.

## METHODS

We used Christmas Bird Count (CBC) data from the north-central United States during the years 1988–2017 to determine (1) whether species experienced changes (declines) in abundance following the appearance of WNV and (2) whether changes in abundance varied by region within our study area. CBCs are citizen-science bird surveys in which volunteers count all birds seen and heard during a 24-h period within an area defined by a circle with a 15-mile (24.1-km) diameter. CBCs are conducted on one day during a period from mid-December through early January. Data from CBCs are subject to bias primarily due to variation in observer effort within and among individual CBCs and the nonrandom distribution of count circles (Sauer 2000). However, CBCs

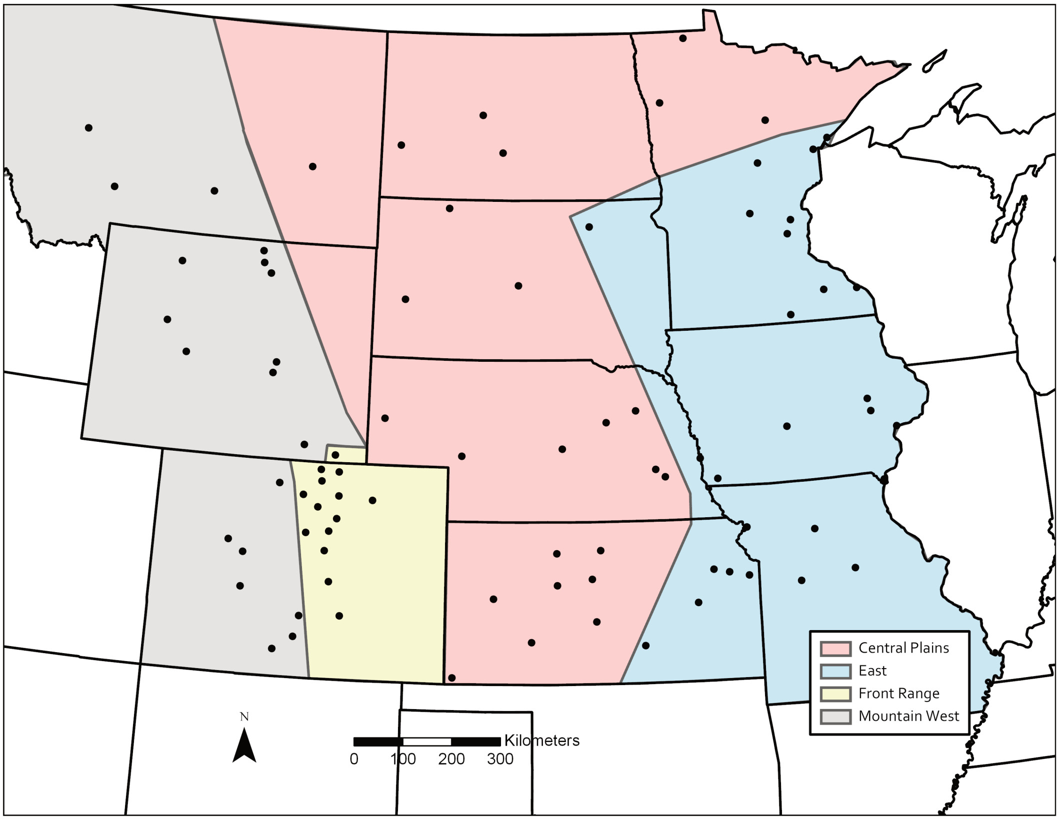

Fig. 1. Study area, ecological regions, and Christmas Bird Count (CBC) circle locations used in analysis.

are one of few long-term avian monitoring programs, and data from the program have been used in hundreds of studies analyzing changes in avian abundance (Temple and Wiens 1989, Dunn et al. 2005).

We chose the time period 1988–2017 because there are nearly an equivalent number of years before and after (14 and 15 years, respectively) the appearance of WNV in the study area, and 1988 is the earliest year that the majority of the CBCs in our study area have available data. We selected CBCs ($n = 84$) with at least 8 years of data prior to 2002 and with at least 9 years of data after 2002. We excluded CBCs with fewer years of record. We retrieved CBC data from the Audubon Society data portal (https://netapp.audubon.org/cbcobservation).

## Study Area

Our study area covered a large portion of the north-central United States that included all or portions of the following states: Minnesota, Iowa, Missouri, Kansas, Nebraska, South Dakota, North Dakota, Montana, Wyoming, and Colorado (Fig. 1). We chose these areas because of a sharp gradient in climatic condition across the study area and because our focal species are found in much or all of this region (see Study Species). Average annual precipitation ranges from 13–48 cm in western portions of our study area to 83–98 cm in the southeastern sections (PRISM Climate Group 2019). Average January temperature ranges from −15 °C to −5 °C in northern portions of our study area to 0 °C to 1 °C in southern sections (PRISM Climate Group 2019). We chose the southern limits of the study area to correspond with the southern limits of selected focal species, specifically Black-billed Magpie and Black-capped Chickadee (*Poecile atricapillus*).

## Study Species

We focused our analysis on Black-billed Magpie (BBMA) and Black-capped Chickadee

(BCCH) because both are known to be vulnerable to WNV and anecdotal evidence suggests that both have declined in our study area. We also selected 2 additional species for analysis that are relatively similar (e.g., year-round residents, similar life history strategies) to each of our focal species. For BBMA we used Blue Jay (BLJA; *Cyanocitta cristata*) and for BCCH we used White-breasted Nuthatch (WBNU; *Sitta carolinensis*) as comparison species. While WBNU has a somewhat different life history than BCCH, no other species in the family Paridae occurs year-round over our entire study area. BLJA is the species in our area most similar to BBMA, as both are corvids and both are relatively social, intelligent, and able to exploit multiple niches. Like other corvids, BLJA has shown high mortality from WNV (Komar et al. 2003), yet a previous study on breeding bird abundances indicated quick recoveries of BLJA populations within a few years after WNV emergence (LaDeau et al. 2007). Thus, in this study we consider BLJA to be moderately susceptible to WNV. We included these additional species to show whether any changes in BBMA or BCCH abundances are linked to some other cause, such as large-scale habitat modification. If causes other than WNV were the source of declines in some species, we would expect to see similar declines or increases in all species regardless of their susceptibility to WNV.

American Crow (AMCR; *Corvus brachyrhynchos*) is another widely distributed corvid that has a well-documented susceptibility to WNV (Caffrey et al. 2005). However, we chose not to include AMCR because concentrations of crows are migratory and/or nomadic in the Great Plains, as wintering populations likely move in response to resource availability (Verbeek and Caffrey 2002, Silcock and Jorgensen 2018b). AMCR CBC totals are highly variable between years across many of our counts, indicating that nomadic movement influences the numbers recorded on individual CBCs.

### Analysis

Our primary interest was to detect any broad changes in winter abundance of our focal and comparison species before and after the arrival of WNV in the north-central United States (2002). We limited our analysis to determining differences in average species abundance pre-WNV (1986–2001) and post-WNV (2003–2018). We performed all statistical tests and analysis in Program R (R Core Team 2018).

We separated our study area into 4 regions to better assess any spatial differences from the impacts of WNV and to examine how different populations of sensitive species responded to the outbreak of the disease. We delineated regions based on 30-year average January temperature, average annual precipitation, elevation, and the range of Black-billed Magpie, our primary species of interest. Our 4 regions were as follows (Fig. 1): (1) East or Eastern (eastern Nebraska, eastern Kansas, Iowa, northwestern Missouri, and eastern Minnesota), (2) Central Plains (western Minnesota, North Dakota, South Dakota, and Nebraska), (3) Mountain West (western Colorado, Wyoming, and Montana), and (4) Front Range (central Colorado). Average January temperature differed between Front Range (−1.36 °C) and Central Plains (−5.0 °C), as well as between Front Range (−1.36 °C) and Mountain West (−4.53 °C). The East differed from all other regions in average annual precipitation (25.0 cm to 10.1–15.4 cm, respectively). While the East and Central Plains have similar average January temperature (−5.42 °C to −5.0 °C), no Eastern CBCs ever recorded a BBMA in any counts made from 1988 to 2017. The CBCs within the Mountain West all occur at high elevations (+1100 m) and contain different habitats compared to the rest of our study area. Much of these regions corresponds with established Bird Conservation Regions (BCRs) defined by the Commission for Environmental Cooperation (CEC 1997). However, many of the CBC circles in the study area overlap multiple BCRs, and the lack of standardization in CBC locations created large disparities between the numbers of circles in one BCR compared to others within our study area. Given the importance of temperature and precipitation to WNV transmission and to our focal species, we chose to group CBCs in this study on additional criteria.

Raw counts of species abundance from CBCs are subject to bias due to varying observer effort and skill as well as weather across years. Therefore, it is necessary to adjust count data to compensate for biases prior to using the data in analysis (Link and Sauer 1999, Hochachka et al. 2004, Link et al. 2006).

The simplest adjustment for effort, such as scaling counts per unit effort (birds per party hour), assumes that more birds will be detected with increased effort. However, counts occur within a confined area regardless of the number of participants, and certain species are likely to be detected at a higher rate than others are (Link and Sauer 1999, Link et al. 2006). Simply scaling by party hour does not take into account the fact that there is a limited number of birds within a circle or the possibility of diminishing returns on the counts of certain species as effort increases (Link et al. 2006).

We modeled CBC counts for each species as an overdispersed Poisson log-linear regression and fit this model using Bayesian hierarchical methods. We adjusted raw counts and modeled for average annual abundance, using the effort adjustment methods introduced by Link and Sauer (1999) and following the Bayesian hierarchical approach presented by Link et al. (2006). Briefly, this model allows estimation of effort parameters and trends from each region to account for the potential differences of effort between areas with low population centers (e.g., western Kansas) and areas with large urban centers and likely higher effort for each count (e.g., Front Range, which included the Denver metropolitan area). Effort and overdispersion parameters are treated as random effects, with stratum-specific effects and regional trend coefficients that are treated as fixed effects (Link et al 2006). We used standard noninformative priors with normal distributions for means and flat gamma distributions for variances on all parameters (Link et al. 2006, 2008). We used the RJAGS package in Program R to implement Markov chain Monte Carlo (MCMC) sampling of posterior distributions of parameters and abundance estimates. We generated chains of length 30,000 and discarded the first 3000 chains as burn-in. Effort coefficients are presented with 95% credible intervals.

We modeled effort-corrected estimated abundances separately for the years before WNV (1988–2001) and after the emergence of WNV (2003–2017). Using the pre-WNV model, we projected abundances with 95% confidence for the years after WNV emergence (2003–2017) by using the existing effort values for the years 2003–2017. We compared these estimated abundances from the pre-WNV model to the "true" observations from the modeled data post-WNV to determine whether winter abundances for each species were within or outside the expected range, given conditions before 2002 (LaDeau et al. 2007). We analyzed the differences between the projected abundances and actual abundances regionally, scaling counts to birds per CBC circle within each of our 4 regions. We calculated annual trends from 1988 to 2017 by using the observed (i.e., not projected) pre-WNV and post-WNV abundances for each circle and then compared the overall trends regionally. We used linear models to test the relationship of the overall abundance trends of each species with average January temperature and average annual precipitation to determine the potential impact of climate patterns on winter abundances.

## RESULTS

BBMA abundances after 2002 were markedly lower than estimated abundances pre-WNV in the Central Plains and the Front Range (Fig. 2). The most consistent and extreme decline in abundances after WNV emergence was observed in the Central Plains. Average BBMA-estimated abundances increased in the Mountain West, with all observed abundances falling within the expected range of estimated abundances, given the observed trajectory pre-WNV (Fig 2). Overall, BBMA winter abundances experienced a 4.32% (±0.7%) annual decline from 1988 to 2017 in the Central Plains. BMMA winter abundances declined by 2.17% (±1.2%) annually in the Front Range and increased by 1.53% (±0.65%) annually in the Mountain West from 1988 to 2017 (Table 1). Annual trends increased with increasing precipitation across all circles ($F_{2,55} = 3.03$, $P = 0.029$). Overall BBMA trends were unaffected by average January temperature.

Observed BCCH abundances were significantly lower than estimated abundances given pre-WNV observations for the 4 years that immediately followed the emergence of WNV (2003–2006) in the Central Plains (Fig. 3). Observed BCCH winter abundances in the Front Range were on the lowest end of the 95% CI of predicted abundances for most years following 2002, suggesting a potential impact of WNV emergence (Fig. 3). In the East and the Mountain West, observed abundances

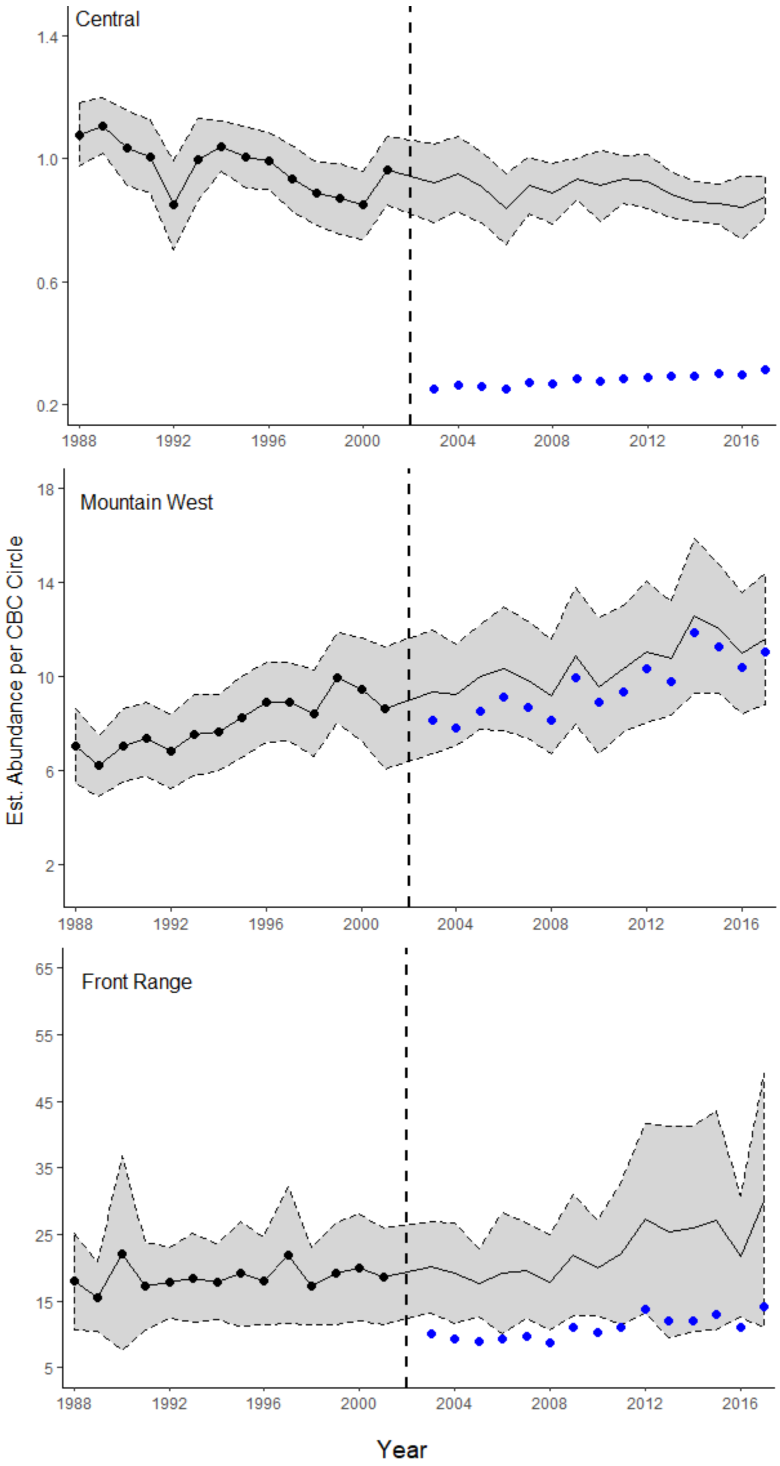

Fig. 2. Black-billed Magpies observed (black circles, before West Nile virus [WNV]; blue circles, after WNV) versus predicted abundances (solid line, with shaded area representing 95% confidence intervals) before and after the emergence of WNV. Predicted values were modeled given conditions before 2002. All abundances are adjusted for effort from the hierarchical model analysis and plotted as the average number of birds per Christmas Bird Count (CBC) circle in each region.

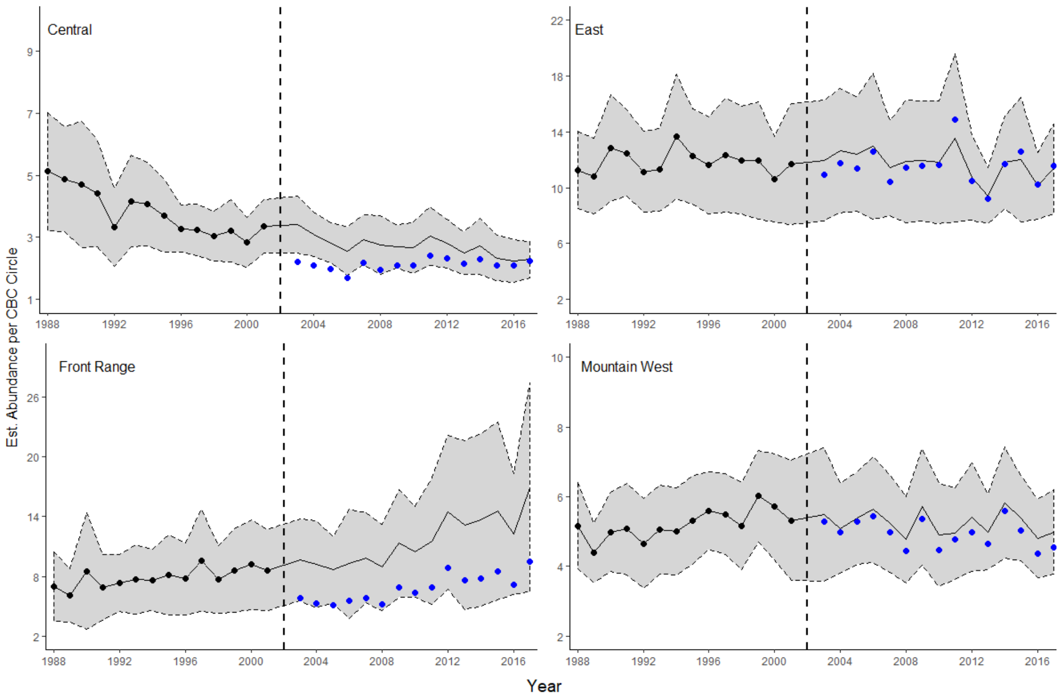

Fig. 3. Black-capped Chickadees observed (black circles, before West Nile virus [WNV]; blue circles, after WNV) versus predicted abundances (solid line, with shaded area representing 95% confidence intervals) before and after the emergence of WNV. Predicted values were modeled given conditions before 2002. All abundances are adjusted for effort from the hierarchical model analysis and plotted as the average number of birds per Christmas Bird Count (CBC) circle in each region.

Table 1. Estimated effort coefficients (*p*, *B*) with 95% credible intervals from a hierarchical model of Black-billed Magpies (top) and Black-capped Chickadee (bottom) winter abundance in the Great Plains, USA. Estimates are from the pre-WNV/projected model for each species. Trend estimates are presented with 95% credible (projected trends given conditions pre-WNV) and confidence (observed trends) intervals from 1988 to 2017.

| Species and region | *p* | *B* | Trend (% change per year) |
|---|---|---|---|
| Black-billed Magpie | | | |
| Central | −0.67 (−0.75, −0.59) | 0.63 (0.59, 0.67) | Projected: −0.93 (−1.52, −0.35)<br>Observed: −4.32 (±0.7) |
| Front Range | 0.55 (0.52, 0.58) | 0.39 (0.37, 0.41) | Projected: 0.05 (−0.02, 0.28)<br>Observed: −2.17 (±1.2) |
| Mountain West | −0.01 (−0.06, 0.03) | 0.88 (0.82, 0.94) | Projected: 1.92 (1.67, 2.17)<br>Observed: 1.53 (±0.65) |
| Black-capped Chickadee | | | |
| East | 0.15 (0.13, 0.17) | 0.89 (0.86, 0.92) | Projected: 0.01 (−0.09, 0.03)<br>Observed: 0.22 (±0.6) |
| Central | −0.14 (−0.17, 0.11) | 0.83 (0.8, 0.86) | Projected: −2.31 (−2.6, −2.0)<br>Observed: −2.57 (±0.8) |
| Front Range | 0.13 (0.10, 0.16) | 1.06 (1.0, 1.12) | Projected: 1.36 (1.02, 1.7)<br>Observed: −0.72 (±1.2) |
| Mountain West | 0.55 (0.48, 0.62) | 0.41 (0.36, 0.45) | Projected: 0.17 (−0.21, 0.43)<br>Observed: −0.87 (±0.8) |

were within the predicted number of birds, given conditions pre-WNV (Fig. 3). From 1988 to 2017, BCCHs declined 2.57% (±0.8%) annually in the Central Plains. Trends were nearly steady in other regions, with 0.72% (±1.2%) and 0.87% (±0.8%) annual declines in the Front Range and the Mountain West, respectively, and a 0.22% (±0.6%) increase in

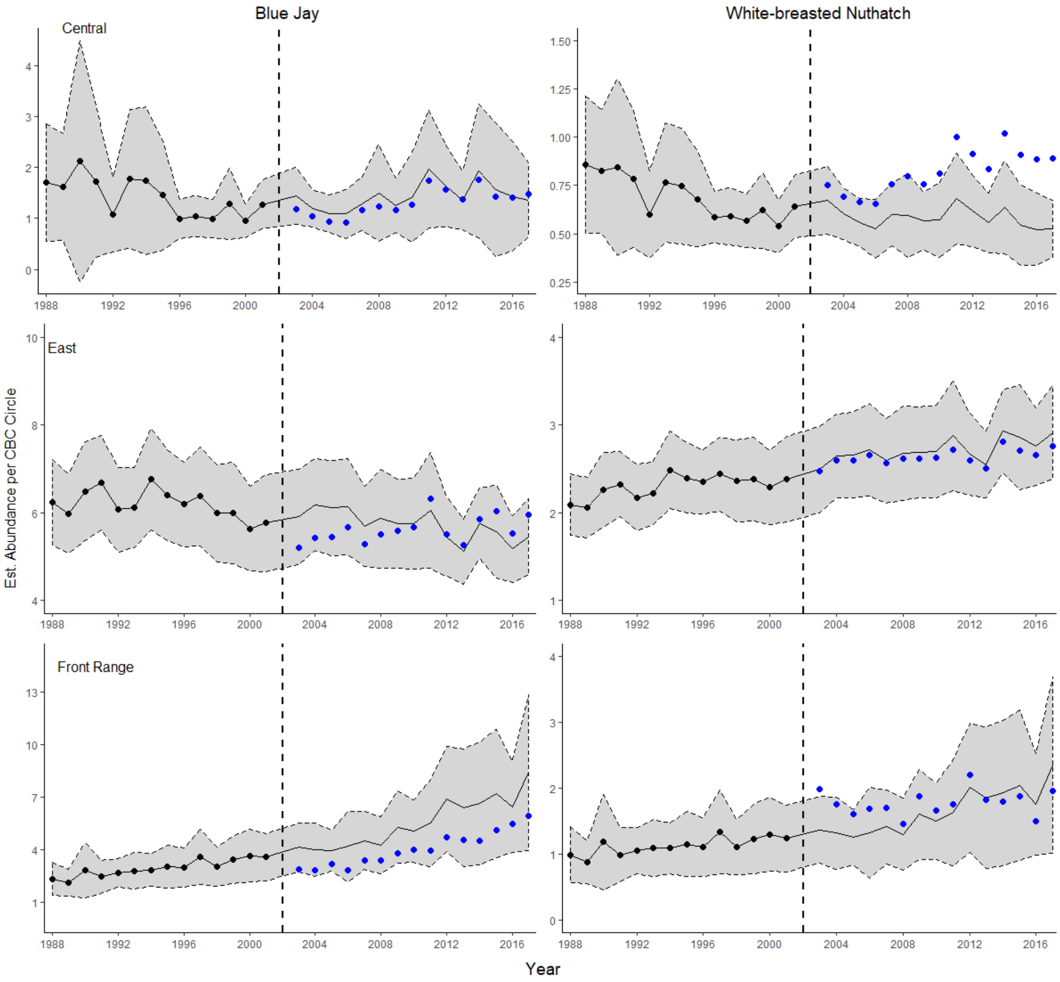

Fig. 4. Blue Jays and White-breasted Nuthatches observed (black circles, before West Nile virus [WNV]; blue circles, after WNV) versus predicted abundances (solid line, with shaded area representing 95% confidence intervals) before and after the emergence of WNV. Predicted values were modeled given conditions before 2002. All abundances are adjusted for effort from the hierarchical model analysis and plotted as the average number of birds per Christmas Bird Count (CBC) circle in each region.

the Eastern region. Overall BCCH abundance trended higher with increasing average precipitation ($F_{2,81} = 2.58$, $P = 0.027$), with no impact of January temperatures.

We detected no change or slight increases in abundances of WBNU and BLJA across the East, the Central Plains, and the Front Range. WBNU trends were generally steady or increasing overall (0.01%–1.2% annually), and post-WNV abundances were well within the predicted range given conditions before the arrival of WNV. In the Central Plains, WBNU abundances climbed above the predicted estimates from 2009 to 2017 given conditions pre-WNV (Fig. 4). BLJA abundances post-WNV were also within the 95% CI of predicted trends given pre-WNV conditions, and this species experienced minor (0.01%–3.4%) but variable (±1.4%) increases across regions (Fig. 4).

## DISCUSSION

Among all species and regions, the BBMA's sharp and immediate decline in the Central Plains following the appearance of WNV stands out as the most noteworthy. Similar, albeit less dramatic, declines by BBMA were also observed in the Front Range, but no change in expected abundance was observed in the Mountain West. BCCH abundances followed a similar pattern, with declines in the Central Plains and the Front Range immediately after the arrival of WNV; however, this species was already declining in this region before 2002 and observed abundances eventually matched predicted pre-WNV abundances. BCCH abundances also did not change in the East or the Mountain West. These regional differences conformed to our expectation that changes in abundance would not be uniform throughout the study area. The lack of change in WBNU abundances met our expectations, as this species is not known to be vulnerable to WNV. The lack of major declines in WBNU also supports our conclusions that WNV is contributing to declines of BBMA and, to a lesser extent, BCCH. We acknowledge that large-scale changes in climate and habitat could also be influencing BBMA and BCCH abundances. However, if these were the only factors, we would expect that shifts in habitat or climate would affect species other than BBMA and BCCH and that changes would be similar across species within each region.

Interactions between climate and disease emergence may be factors in BBMA population declines and may contribute to ongoing declines of BCCH. Annual abundance for BBMA and BCCH increased with increasing annual precipitation across the 84 circles in our region. Warmer winters and drier years increase WNV transmission (Epstein 2001, Deichmeister and Telang 2011), which would explain why the most southern and low-elevation ecological zones in our study saw the largest declines in BBMA abundances. Furthermore, the Front Range and the Central Plains include areas with high rates of human WNV incidence, indicating high exposure of the disease to vulnerable bird species as well (CDCP 2019). Additionally, BBMA distribution in the United States is likely limited by temperature, and daily activity is restricted by high temperatures (Bock and Lepthien 1975, Kelly et al. 2004). These limitations would explain why the circles within the Mountain West, areas with consistently cooler temperatures and higher precipitation than observed in the Central Plains, showed increasing BBMA abundances both before and after WNV emergence. However, our basic models that tested the effects of average temperature and average annual precipitation on 30-year abundance trends over such large areas may not fully account for climate impacts on each species, particularly at smaller scales. Increasing temperatures across regions could be limiting BBMA numbers both by creating individual thermal tolerance challenges and by increasing WNV transmission.

We acknowledge that our analysis encompasses an extremely large geographic area, with relatively few CBCs given the size of the regions as a whole. This lack of CBCs is mostly due to the low human population over much of the study area, especially the Central Plains. Thus, the trends from each region are unlikely to capture small-scale changes in abundance that may be occurring counter to our results. More precise regional data and targeted surveys would better illuminate the apparent declines in wintering BBMA and BCCH. However, the limited coverage given the large geographic area may also explain why such large declines occurred without much notice, and the overall lack of studies over much of the study area is another justification for our initial efforts at addressing BBMA declines.

Our results indicate that WNV is likely having consequential impacts on certain avian species nearly 2 decades after its introduction into the Western Hemisphere. The particularly dramatic decline of BBMA in the Central Plains is evident at the individual count level in many circles within this region. For example, the Lake McConaughy CBC in western Nebraska tallied an average of 82.4 (SE = 10.0) BBMAs during the period 1991–2002, but from 2003 to 2018, the average number of BBMAs recorded dropped to 21.5 (SE = 3.2). Similarly, the same CBC averaged 39.6 (SE = 15.5) and 7.6 (SE = 2.9) BCCHs during the same 2 periods. The overall decline (2.57% annual decrease) in BCCH abundances and BBMA abundances (4.32% annual decline) in the Central Plains is a troubling indication of the declining number of birds in the Great Plains. Future work should continue to monitor the winter abundances and associated trends of these species in this region and recognize the multiple risks that species at low abundances face, particularly the risks of emerging diseases and shifting climates.

## ACKNOWLEDGMENTS

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## LITERATURE CITED

ATKINSON, C.T., K.L. WOODS, R.J. DUSEK, L.S. SILEO, AND W.M. IKO. 1995. Wildlife disease and conservation in Hawaii: pathogenicity of avian malaria (*Plasmodium relictum*) in experimentally infected Iiwi (*Vestiaria coccinea*). Parasitology 111:S59–S69.

BELL, J.A., C.M. BREWER, N.J. MICKELSON, G.W. GARMAN, AND J.A. VAUGHAN. 2006. West Nile virus epizootiology, central Red River Valley, North Dakota and Minnesota, 2002–2005. Emerging Infectious Diseases 12:1245–1247.

BOCK, C.E., AND L.W. LEPTHIEN. 1975. Distribution and abundance of the Black-billed Magpie (*Pica pica*) in North America. Great Basin Naturalist 35:269–272.

CAFFREY, C., C.R. SMITH, AND T.J. WESTON. 2005. *West Nile virus* devastates an American Crow population. Condor 107:128–132.

CAMPBELL, G.L., A.A. MARFIN, R.S. LANCIOTTI, AND D.J. GUBLER. 2002. West Nile virus. *The Lancet* Infectious Diseases 2:519–529.

[CDCP] CENTERS FOR DISEASE CONTROL AND PREVENTION. 2019. West Nile virus: final cumulative maps and data for 1999–2018. National Center for Emerging and Zoonotic Infectious Diseases (NCEZID), Division of Vector-Borne Diseases (DVBD); [accessed 1 December 2019]. https://www.cdc.gov/westnile/statsmaps/cumMapsData.html#one

[CEC] COMMISSION FOR ENVIRONMENTAL COOPERATION. 1997. Ecological regions of North America: toward a common perspective. Commission for Environmental Cooperation, Montreal, Canada. 71 pp.

CONOVER, M.R., AND A.J. ROBERTS. 2016. Declining populations of Greater Sage-Grouse: where and why. Human–Wildlife Interactions 10:217–229.

DEGROOTE, J.P., R. SUGUMARAN, S.M. BREND, B.J. TUCKER, AND L.C. BARTHOLOMAY. 2008. Landscape, demographic, entomological, and climatic associations with human disease incidence of West Nile virus in the state of Iowa, USA. International Journal of Health Geographics 7:art19. 16 pp.

DEICHMEISTER, J.M., AND A. TELANG. 2011. Abundance of West Nile virus mosquito vectors in relation to climate and landscape variables. Journal of Vector Ecology 36:75–85.

DUNN, E.H., C.M. FRANCIS, P.J. BLANCHER, S.R. DRENNAN, M.A. HOWE, D. LEPAGE, C.S. ROBBINS, K.S. ROSENBERG, J.R. SAUER, AND K.G. SMITH. 2005. Enhancing the scientific value of the Christmas Bird Count. Auk 122:338–346.

EPSTEIN, P.R. 2001. West Nile virus and the climate. Journal of Urban Health 78:367–371.

EZENWA, V.O., L.E. MILHEIM, M.F. COFFEY, M.S. GODSEY, R.J. KING, AND S.C. GUPTILL. 2007. Land cover variation and West Nile virus prevalence: patterns, processes, and implications for disease control. Vector-Borne and Zoonotic Diseases 7:173–180.

FOPPA, I.M., R.H. BEARD, AND I.H. MENDENHALL. 2011. The impact of West Nile virus on the abundance of selected North American birds. BMC Veterinary Research 7:art43. 9 pp.

GEORGE, T.L., R.J. HARRIGAN, J.A. LAMANNA, D.F. DESANTE, J.F. SARACCO, AND T.B. SMITH. 2015. Persistent impacts of West Nile virus on North American bird populations. Proceedings of the National Academy of Sciences 112:14290–14294.

GUBLER, D.J. 2007. The continuing spread of West Nile virus in the western hemisphere. Clinical Infectious Diseases 45:1039–1046.

HAYES, E.B., N. KOMAR, R.S. NASCI, S.P. MONTGOMERY, D.R. O'LEARY AND G.L. CAMPBELL. 2005. Epidemiology and transmission dynamics of West Nile virus disease. Emerging Infectious Diseases 11:1167–1173.

HOCHACHKA, W.A., A.A. DHONDT, K.J. MCGOWAN, AND L.D. KRAMER. 2004. Impact of West Nile virus on American Crows in the northeastern United States, and its relevance to existing monitoring programs. EcoHealth 1:60–68.

KELLY, A., B.J. GODLEY, AND R.W. FURNESS. 2004. Magpie, *Pica pica*, at the southern limit of their range actively select thermal environment at high ambient temperatures. Zoology in the Middle East 32:13–26.

KOMAR, N. 2003. West Nile virus: epidemiology and ecology in North America. Advances in Virus Research 61: 185–234.

KOMAR, N., S. LANGEVIN, S. HINTEN, N.M. NEMETH, E. EDWARDS, D.L. HETTLER, B.S. DAVIS, R.A. BOWEN, AND M.L. BUNNING. 2003. Experimental infection of North American birds with the New York 1999 strain of West Nile virus. Emerging Infectious Diseases 9:311–322.

KOMAR, N., N.A. PANELLA, S.A. LANGEVIN, A.C. BRAULT, M. AMADOR, E. EDWARDS, AND J.C. OWEN. 2005. Avian hosts for West Nile virus in St. Tammany Parish, Louisiana, 2002. American Journal of Tropical Medicine and Hygiene 73:1031–1037.

LADEAU, S.L., A.M. KILPATRICK, AND P.P. MARRA. 2007. West Nile virus emergence and large-scale declines of North American bird populations. Nature 447: 710–713.

LANDESMAN, W.J., B.F. ALLAN, R.B. LANGERHANS, T.M. KNIGHT, AND J.M. CHASE. 2007. Inter-annual associations between precipitation and human incidence of West Nile virus in the United States. Vector-Borne and Zoonotic Diseases 7:337–343.

LINK, W.A., AND J.R. SAUER. 1999. Controlling for varying effort in count surveys: an analysis of Christmas Bird Count data. Journal of Agricultural, Biological, and Environmental Statistics 4:116–125.

LINK, W.A., J.R. SAUER, AND D.K. NIVEN. 2006. A hierarchical model for regional analysis of population change using Christmas Bird Count data, with application to the American Black Duck. Condor 108: 13–24.

LINK, W.A., J.R. SAUER, AND D.K. NIVEN. 2008. Combining breeding bird survey and Christmas Bird Count data to evaluate seasonal components of population change in Northern Bobwhite. Journal of Wildlife Management 72:44–51.

MOLLHOFF, W.J. 2016. The second Nebraska breeding bird atlas. Bulletin of University of Nebraska State

Museum, Volume 29. University of Nebraska State Museum, Lincoln, NE. 304 pp.

[NOAA] NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION. 2019. Statistical weather and climate information. [Accessed 18 September 2019]. https://www.ncdc.noaa.gov/climate-information/statistical-weather-and-climate-information

PRISM CLIMATE GROUP. 2019. PRISM climate data. Oregon State University, Corvallis, OR; [accessed 14 November 2019]. http://prism.oregonstate.edu

R CORE TEAM. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing,Vienna, Austria. https://www.R-project.org

RAPPOLE, J.H., AND Z. HUBALEK. 2003. Migratory birds and West Nile virus. Journal of Applied Microbiology 94:47S–58S.

SAUER, J.R. 2000. A critical look at national monitoring programs for birds and other wildlife species. Pages 80–86 *in* T. O'Shea and M. Bogan, editors, Interim report of the workshop on monitoring trends in U.S. bat populations. U.S. Geological Survey, Fort Collins, CO.

SILCOCK, W.R., AND J.G. JORGENSEN. 2018a. Black-billed Magpie (*Pica hudsonia*), version 1.0. *In*: Birds of Nebraska—online. [Accessed 23 September 2019]. www.BirdsofNebraska.org

SILCOCK, W.R., AND J.G. JORGENSEN. 2018b. American Crow (*Corvus brachyrhynchos*), version 1.0. *In*: Birds of Nebraska—online. [Accesed 23 September 2019]. www.BirdsofNebraska.org

STAUFFER, G.E., D.A. MILLER, L.M. WILLIAMS, AND J. BROWN. 2018. Ruffed Grouse population declines after introduction of West Nile virus. Journal of Wildlife Management 82:165–172.

TEMPLE, S.A., AND J.A. WIENS. 1989. Bird populations and environmental changes: can birds be bio-indicators. American Birds 43:260–270.

VERBEEK, N.A., AND C. CAFFREY. 2002. American Crow (*Corvus brachyrhynchos*), version 2.0. *In:* A.F. Poole and F.B. Gill, editors, The birds of North America. Cornell Lab of Ornithology, Ithaca, NY. https://birdsna.org/Species-Account/bna/species/amecro/introduction

WHEELER, S.S., C.M. BARKER, Y. FANG, M.V. ARMIJOS, B.D. CARROLL, S. HUSTED, W.O. JOHNSON, AND W.K. REISEN. 2009. Differential impact of West Nile virus on California birds. Condor 111:1–20.

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