

LETTERS

West Nile virus emergence and large-scale declines of North American bird populations

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Emerging infectious diseases present a formidable challenge to the conservation of native species in the twenty-first century¹. Diseases caused by introduced pathogens have had large impacts on species abundances², including the American chestnut³, Hawaiian bird species⁴ and many amphibians⁵. Changes in host population sizes can lead to marked shifts in community composition and ecosystem functioning^{3,4,6}. However, identifying the impacts of an introduced disease and distinguishing it from other forces that influence population dynamics (for example, climate⁷) is challenging and requires abundance data that extend before and after the introduction^{2,5}. Here we use 26 yr of Breeding Bird Survey (BBS)⁸ data to determine the impact of West Nile virus (WNV) on 20 potential avian hosts across North America. We demonstrate significant changes in population trajectories for seven species from four families that concur with a priori predictions and the spatio-temporal intensity of pathogen transmission. The American crow population declined by up to 45% since WNV arrival, and only two of the seven species with documented impact recovered to pre-WNV levels by 2005. Our findings demonstrate the potential impacts of an invasive species on a diverse faunal assemblage across broad geographical scales, and underscore the complexity of subsequent community response.

Seven years after the emergence of WNV in New York City in 1999, the population-level impacts of this disease on wild birds remain

largely unknown^{9,10}. Tens of thousands of dead individuals from wild, zoo and pet populations have tested positive for WNV across North America¹¹, and challenge experiments have demonstrated interspecific variability in mortality rates under laboratory conditions¹². Early field studies documented mortality in some species^{13,14} and evidence of spatially heterogeneous fluctuations^{9,15,16}, but overall population patterns were inconclusive. Our study tests the hypothesis that WNV has caused significant population declines in a broad taxonomic range of avian hosts across North America. We explicitly considered variability in host susceptibility, spatio-temporal heterogeneity in pathogen transmission, and impacts on populations.

To test this hypothesis, we developed a set of independent predictions of WNV impact for 20 species of birds from 11 families on the basis of published laboratory infection experiments, mosquito feeding studies and seroprevalence surveys (Table 1 and Supplementary Table 1). Target species span a range of expected impacts, from crows with high mortality to gray catbirds and mourning doves, which seem to tolerate infection without significant morbidity^{12,17}. Additionally, we chose five species (Baltimore oriole, chipping sparrow, eastern bluebird, eastern towhee and white-breasted nuthatch) that have not been the focus of previous work to assess potential disease impacts on a broader community. We then used a bayesian hierarchical regression fit to 26 yr of survey data to test these species-specific predictions across the large geographical scale represented by WNV emergence in North America.

Table 1 | Predicted and observed impact of WNV, climate influence and 10- and 26-yr minimum abundances

Species	Predicted impact	Observed impact	Change in DIC with climate (%)	Minimum abundance	
				10-yr	26-yr
American crow (<i>Corvus brachyrhynchos</i>)	High	Yes	4.6	2004*	2004*
Blue jay (<i>Cyanocitta cristata</i>)	High	Yes	-14.5‡	2004*	2004*
Fish crow (<i>Corvus ossifragus</i>)	High	No	0.01	2005*	2005*
Tufted titmouse (<i>Baeolophus bicolor</i>)	High	Yes	-1.1‡	2004*	1980
American robin (<i>Turdus migratorius</i>)	Moderate	Yes	5.7	2005*	1981
House wren (<i>Troglodytes aedon</i>)	Moderate	Yes	0.1	2003*	2003*
Chickadee† (<i>Poecile</i> spp.)	Moderate	Yes	-23.8‡	1996	1985
Common grackle (<i>Quiscalus quiscula</i>)	Moderate	No	0	2003*	2003*
Northern cardinal (<i>Cardinalis cardinalis</i>)	Moderate	No	2.1	1997	1980
Song sparrow (<i>Melospiza melodia</i>)	Moderate	No	-5.4‡	2004*	2004*
Downy woodpecker (<i>Picoides pubescens</i>)	Low	No	-1.0‡	2003*	1984
Gray catbird (<i>Dumetella carolinensis</i>)	Low	No	-1.2‡	1997	1986
Mourning dove (<i>Zenaidura macroura</i>)	Low	No	-1.8‡	1997	1980
Northern mockingbird (<i>Mimus polyglottos</i>)	Low	No	0.4	1997	1997
Wood thrush (<i>Hylacichla mustelina</i>)	Low	No	0.1	2003*	2003*
Eastern bluebird (<i>Sialia sialis</i>)	Unknown	Yes	0.4	2003*	1980
Baltimore oriole (<i>Icterus galbula</i>)	Unknown	No	4.4	2004*	2004*
Chipping sparrow (<i>Spizella passerina</i>)	Unknown	No	4.3	1997	1980
Eastern towhee (<i>Pipilo erythrophthalmus</i>)	Unknown	No	-1.2‡	2004*	1991
White-breasted nuthatch (<i>Sitta carolinensis</i>)	Unknown	No	0.2	1996	1984

See Supplementary Table 1 for full details of predicted impact data. Impact of WNV is measured as abundance below 95% CIs after WNV arrival. Data are for 20 North American bird species.

* The indicated years follow peak human WNV epidemics in the United States (2002–03).

† Black-capped (*Poecile atricapilla*) and Carolina chickadee (*Poecile carolinensis*) numbers were combined, as species-specific data are unreliable in areas of range overlap.

‡ Negative values for deviance information criterion (DIC) indicate improved model fit with inclusion of climate for these species.

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Thirteen of the twenty species studied reached 10-yr population lows after the large-scale human WNV epidemics that occurred in much of the United States in 2002–03 (ref. 11) ($P = 0.002$, assuming probability of 10-yr low after 2002 = 0.30), and eight recorded their lowest abundance over the 26 yr studied ($P = 0.001$, assuming probability of 26-yr low after 2002 = 0.12) (Table 1 and Fig. 1). However, to determine whether WNV was involved in these declines, changes in abundance must be evaluated in the context of long-term trends, climate and habitat availability. We included climate variability (El Niño/Southern Oscillation) in final population models for eight species for which model fit was significantly improved (Table 1 and Supplementary Information). We did not include a land-use component in the population model and thus, are unable to rule out a potentially confounding role of changes in land cover during this study (but see below).

Observed abundances after WNV emergence were significantly lower than expected given two decades of population variability for seven species across multiple geographical regions (Figs 2 and 3). Six of these species were independently predicted to suffer high or moderate impacts, and the seventh was previously unstudied (Table 1). These seven species included two members of the family Corvidae (American crow and blue jay), two from Turdidae (American robin and eastern bluebird), two from Paridae (chickadees and tufted titmouse) and one from Troglodytidae (house wren). Population deviations (average difference between modelled and observed abundances) were highly correlated with categorical predicted impacts for the 15 species with prior information (Supplementary Information; $r = -0.67$, $n = 15$, $P = 0.007$). All seven of these species are peridomestic, with known suburban association^{8,18}. Thus, the declines observed for these species are opposite from expectations given continued suburbanization after 1999¹⁹, but are consistent with impacts owing to WNV.

Observed impacts included steep and sometimes progressive multi-year declines in regional populations of American crows (Fig. 2), American robins, chickadees and eastern bluebirds, which were all increasing before WNV arrival (Fig. 1). Other species, including blue jays, tufted titmice and house wrens showed strong 1- or 2-yr declines after intense WNV epidemics, but little or no impacts at other times. Regionally, we found significant deviations from expected abundances for all seven species in the eastern United States (Figs 2 and 3). In other areas where WNV has been present for fewer years, the intensity of impact varied among species (Supplementary Fig. 1). Common grackle populations in Maryland declined significantly after WNV emergence in that state, although in other regions this species remained at expected abundances (Supplementary Fig. 2).

The intensity of declines after pathogen emergence was most marked in American crows (Fig. 2). By 2005, crow abundances had declined regionally by up to 45% from 1998 levels, although they had increased steadily for two decades. American crow declines were positively correlated with the intensity of human WNV epidemics within each region ($r = -0.56$, $n = 21$, $P = 0.0003$), despite variability in human behaviour and feeding of mosquitoes on humans compared with birds^{11,17,20}. Similar correlations between human infections and impacts on other avian species were strongest for house wrens and eastern bluebirds ($P < 0.002$), marginally significant for tufted titmouse, American robins and chickadees ($0.05 < P < 0.10$), and non-significant for blue jays ($P = 0.34$; Supplementary Table 2) and the 13 species without detectable WNV impact (P -values > 0.1).

Similarly, the intensity of WNV impacts on these six affected species was not always consistent across species or regions (Fig. 3). American robin, eastern bluebird and tufted titmouse populations remained below expected abundance across their entire ranges in 2005. Deviations in chickadee populations were significantly reduced in the east but not at their western range limits. Neither house

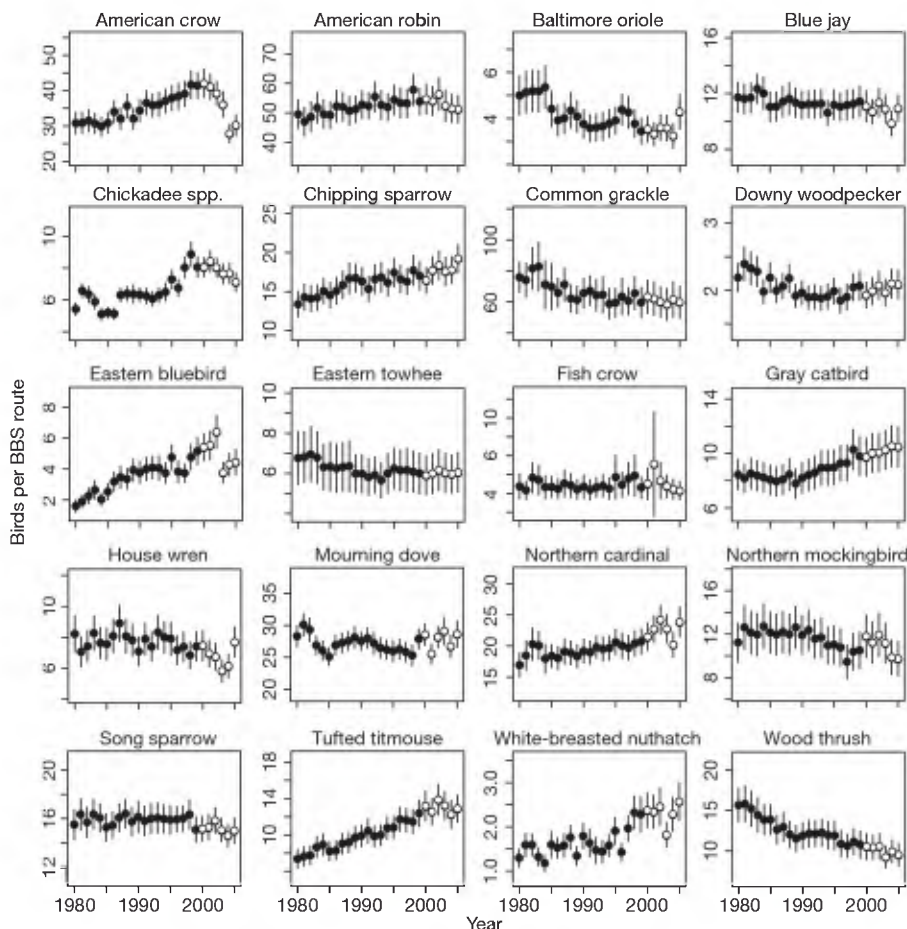


Figure 1 | Time series of mean abundance per BBS route adjusted for missing observations and observer variance. Error bars show 2 standard errors. Open circles denote years after WNV was first detected in North America. Population growth rates between 1980 and 1998 that were significantly different from 0: American crow (95% CI for linear trends (0.014, 0.020)), American robin (0.06, 0.010), Black-capped and Carolina chickadees (0.003, 0.012), chipping sparrow (0.118, 0.175), eastern bluebird (0.046, 0.060), northern cardinal (0.006, 0.011), tufted titmouse (0.026, 0.033), white-breasted nuthatch (0.014, 0.028), Baltimore oriole (−0.0016, −0.006), common grackle (−0.022, −0.014) and wood thrush (−0.023, −0.017).

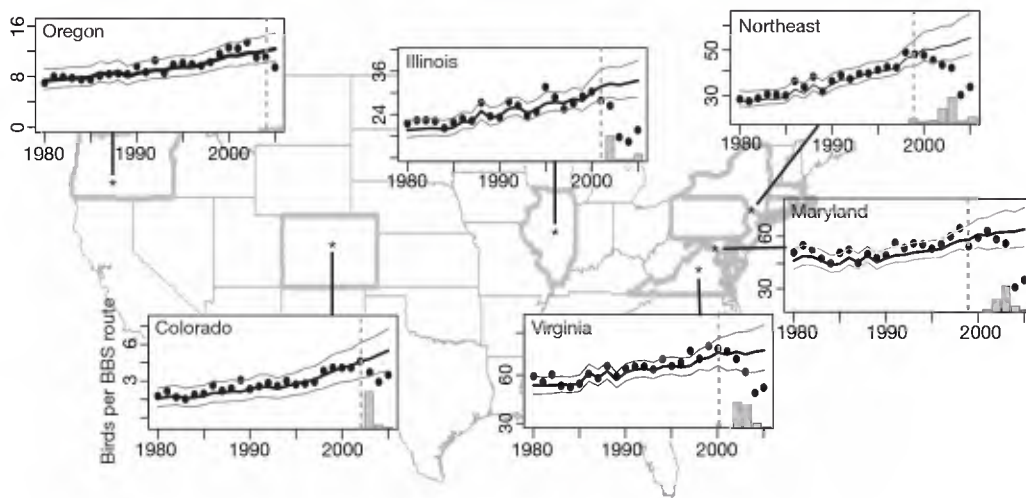


Figure 2 | Declining American crow populations. Observed abundances (circles) versus mean posterior estimates (solid line, with 95% CIs) by region across North America are shown. Values on the y axis are the average number of birds observed per BBS route adjusted for observer differences and missing data. Shaded histograms show numbers of reported annual human infections¹¹ per region (maximum cases per year in northeast, 370; Maryland, 73; Virginia, 29; Illinois, 884; Colorado, 2,947; and Oregon, 7). Vertical dotted lines denote the initial detection of WNV in birds, mosquitoes or humans¹¹.

wren nor blue jay populations showed significant declines in Virginia, whereas abundances were up to 22% and 26% below that expected in other regions before recovering in 2005 (Supplementary Information).

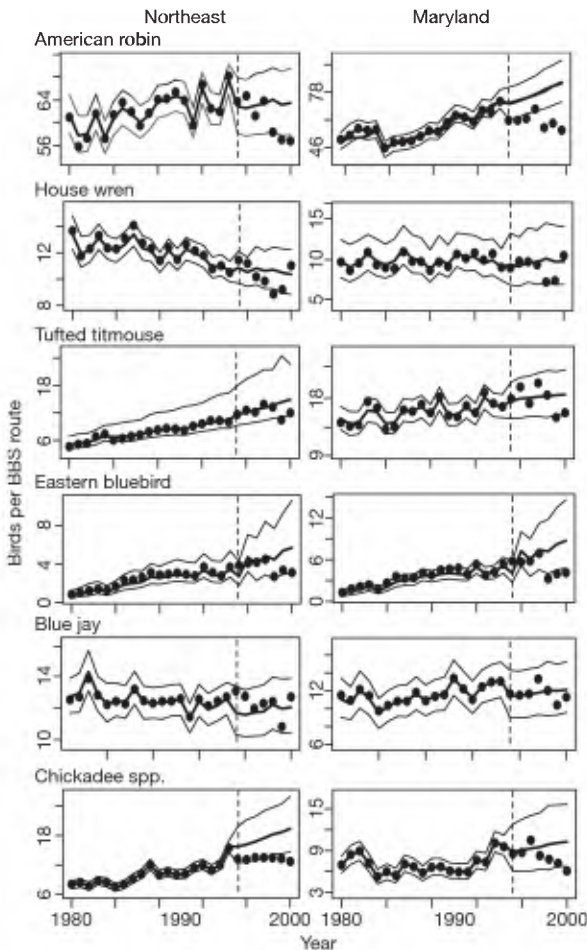


Figure 3 | Population declines and WNV epidemics in the northeastern United States and Maryland. Observed abundances (circles; birds observed per BBS route) versus mean posterior estimated population abundances (solid line, with 95% CIs) for six impacted species are shown. The vertical dotted lines denote the initial detection of WNV in birds, mosquitoes or humans¹¹. The complete version of this figure presents observed and expected abundances for each species in each geographical region where it is present (Supplementary Fig. 1).

Assessing the impacts of an invasive pathogen on host populations across a continent requires difficult assumptions regarding exposure rates, and analyses that are correlational in nature. We approached these challenges by using two decades of local population surveys and climate data to predict species abundance distributions in all years after WNV was first identified. We further strengthened our conclusions by comparing our results to the species-specific impacts predicted from a collection of previous studies (Table 1 and Supplementary Table 1) and to the spatial and temporal pattern in human epidemics (Fig. 2 and Supplementary Table 2). We detected significant declines for six species predicted to have high or moderate WNV impacts, and did not detect declines in the five species with predicted low impact. Additionally, we identified sudden and significant declines in eastern bluebird populations, highlighting the possibility that species that have not been studied with respect to WNV may also be affected by this disease. The fact that we did not detect declines in the eight other species, which appeared to persist at the same abundance or even show increased abundance in the presence of WNV (Baltimore oriole, chipping sparrow, eastern towhee, northern cardinal, white-breasted nuthatch), suggests that the impacts of WNV were relatively low or that detection of population declines may have been masked by regional variability in population fluctuations or long term declines (common grackle, fish crow, song sparrow).

After significantly low abundances, both blue jays and house wrens returned to expected population levels in 2005. The resiliency of species and the lasting impact of WNV will ultimately depend on the species-specific interactions between susceptibility, exposure and intrinsic population growth rates. The rank of observed impacts in corvids is consistent with susceptibility to experimental WNV infection studies, which suggest that American crows suffer the greatest mortality (100%), followed by blue jays (75%) and then fish crows (53%)¹². Such interspecific differences in pathogen effects on populations have been observed in other disease systems^{7,21} and can result in important changes in community composition.

The spatial heterogeneity in disease impact apparent for some species may reflect underlying regional differences in the intensity of viral transmission. Several key factors in WNV transmission are known to vary across the continental United States, including the dominant enzootic vectors²², the relationships between vector abundance and land use²³, and differences in the composition of host communities that can, in turn, influence mosquito feeding preferences²⁰. The role of these and other factors in determining WNV transmission and exposure among hosts is an important topic for future research.

Changes in population abundance such as those documented in this study may themselves alter WNV transmission dynamics^{20,24}. Mortality is likely to facilitate WNV amplification because the

infectiousness of hosts (magnitude of viraemia and length of viral shedding) is greater in individuals that die relative to those that survive¹², and hosts that die from infections are not present as immune or dead-end hosts. Mortality also increases the vector to host ratio, which increases the reproductive ratio of the pathogen, R_0 . Decreases in host abundance may have other impacts on WNV transmission. For example, decreases in the abundance of American robins, which appear to be an important WNV amplification host in several regions of the USA^{17,25}, have been linked to higher incidences of mosquitoes feeding on humans and intensified human WNV epidemics²⁰.

The impacts of invasive pathogens compound existing stressors and create formidable challenges for protecting native wildlife^{1,26}. West Nile virus will continue to affect avian communities in the foreseeable future, and substantial ecosystem effects may become evident with time. Finally, we believe that the findings presented here are probably conservative estimates of population-level impacts because the hardest hit avian sub-populations may reside outside the BBS survey areas, which are limited to secondary roads and generally exclude urban centres where the predominant *Culex* mosquito vectors in the eastern United States are most common. Nonetheless, the population changes that we have documented have already led to marked changes in the composition of avian communities across North America.

METHODS SUMMARY

We selected 20 common North American bird species that were regularly present along survey routes in the northeastern United States where WNV first emerged. We further chose species with available background information regarding susceptibility to WNV infection (Supplementary Information), and selected the species pool to cover the range of expected mortality. Finally, we randomly selected five species from the group that satisfied our general survey criteria but had not been previously studied with regard to WNV. This produced a total of 20 species, which was chosen as the number that we could efficiently model and evaluate.

We used 26 yr of North American BBS⁸ data (1980–2005) for each of the species selected. We included data from an average of 38 routes (range 15–88) and 1,900 distinct census points per region (selected to represent WNV dispersal westward from its east coast introduction) so that the patterns we detected would represent regional population changes, rather than local-scale stochasticity^{9,15,16}. We used a hierarchical bayesian regression model²⁷ fit to data collected before the emergence of WNV to estimate probability distributions for expected abundance in all subsequent years to 2005. Posterior distributions for expected abundance explicitly incorporated trends before WNV emergence and regional climate variability (Supplementary Information), as well as stochasticity associated with location and observation error. We considered a species to have been significantly affected when observed abundances fell outside 95% credible intervals (95% CIs) from the posterior abundance distributions. We validated our results by comparing the species-specific deviations from expected population abundances with predicted WNV impacts based on a collection of previous exposure and mortality studies. Finally, we evaluated the agreement between the timing of our estimated WNV impacts with known WNV presence in a region (first documented and human epidemics).

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

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- Daszak, P., Cunningham, A. A. & Hyatt, A. D. Emerging infectious diseases of wildlife—threats to biodiversity and human health. *Science* 287, 443–449 (2000).
- Hochachka, W. M. & Dhondt, A. A. Density-dependent decline of host abundance resulting from a new infectious disease. *Proc. Natl Acad. Sci. USA* 97, 5303–5306 (2000).
- Paillet, F. L. Chestnut: history and ecology of a transformed species. *J. Biogeogr.* 29, 1517–1530 (2002).
- Van Riper, C. III, Van Riper, S. G., Goff, M. L. & Laird, M. The epizootiology and ecological significance of malaria in Hawaiian (USA) land birds. *Ecol. Monogr.* 56, 327–344 (1986).
- Lips, K. R. et al. Emerging infectious disease and the loss of biodiversity in a Neotropical amphibian community. *Proc. Natl Acad. Sci. USA* 103, 3165–3170 (2006).
- Hooper, D. U. et al. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecol. Monogr.* 75, 3–35 (2005).
- Daszak, P. et al. Amphibian population declines at savannah river site are linked to climate, not chytridiomycosis. *Ecology* 86, 3232–3237 (2005).
- Sauer, J. R., Hines, J. E. & Fallon, J. The North American Breeding Bird Survey, Results and Analysis 1966–2005. Version 6.2. 2006 (<http://www.mbr-pwrc.usgs.gov/bbs/bbs.html>) (2005).
- Caffrey, C. & Peterson, C. C. Christmas bird count data suggest West Nile virus may not be a conservation issue in Northeastern United States. *Am. Birds* 57, 14–21 (2003).
- Marra, P. P. et al. West Nile virus and wildlife. *Bioscience* 54, 393–402 (2004).
- Center for Disease Control and Prevention. West Nile virus: Statistics, surveillance, and control (<http://www.cdc.gov/ncidod/dvbid/westnile/surv&control.htm>) (2006).
- Komar, N. et al. Experimental infection of North American birds with the New York 1999 strain of West Nile virus. *Emerg. Infect. Dis.* 9, 311–322 (2003).
- Caffrey, C., Smith, S. C. R. & Weston, T. J. West Nile virus devastates an American crow population. *Condor* 107, 128–132 (2005).
- Naugle, D. E. et al. West Nile virus: pending crisis for greater sage-grouse. *Ecol. Lett.* 7, 704–713 (2004).
- Bonter, D. & Hochachka, W. M. Combined data of project FeederWatch and the Christmas bird count indicate declines of chickadees and corvids: possible impacts of West Nile virus. *Am. Birds* 57, 22–25 (2003).
- Hochachka, W. M., Dhondt, A. A., McGowan, K. J. & Kramer, L. D. Impact of West Nile virus on American crows in the northeastern United States, and its relevance to existing monitoring programs. *Ecohealth* 1, 60–68 (2004).
- Kilpatrick, A. M., Daszak, P., Jones, M. J., Marra, P. P. & Kramer, L. D. Host heterogeneity dominates West Nile virus transmission. *Proc. R. Soc. B* 273, 2327–2333 (2006).
- Marzluff, J. M., Bowman, R. & Donnelly, R. E. (eds) *Avian Conservation and Ecology in an Urbanizing World* (Kluwer, New York, New York, 2001).
- Acevedo, W., Taylor, J. L., Hester, D. J., Mladinich, C. S. & Glavac, S. (eds) *Rates, Trends, Causes, and Consequences of Urban Land-Use Change in the United States* (US Geological Survey, Denver, Colorado, 2006).
- Kilpatrick, A. M., Kramer, L. D., Jones, M. J., Marra, P. P. & Daszak, P. West Nile virus epidemics in North America are driven by shifts in mosquito feeding behavior. *PLoS Biol.* 4, e82 (2006).
- Atkinson, C. T., Lease, J. K., Drake, B. M. & Shema, N. P. Pathogenicity, serological responses, and diagnosis of experimental and natural malarial infections in native Hawaiian thrushes. *Condor* 103, 209–218 (2001).
- Turell, M. J., Sardelis, M. R., O'Guinn, M. L. & Dohm, D. J. in *Japanese Encephalitis and West Nile Viruses* Vol. 267 Current Topics in Microbiology and Immunology (eds Mackenzie, J., Barrett, A. & Deubel, V.) 241–252 (Springer, Berlin, 2002).
- Spielman, A. & D'Antonio, M. *Mosquito: a natural history of our most persistent and deadly foe* (Hyperion, New York, 2001).
- Reisen, W. K. et al. Role of corvids in epidemiology of West Nile virus in southern California. *J. Med. Entomol.* 43, 356–367 (2006).
- Molaei, G., Andreadis, T., Armstrong, P., Anderson, J. & Vossbrinck, C. Host feeding patterns of *Culex* mosquitoes and West Nile virus transmission, northeastern United States. *Emerg. Infect. Dis.* 12, 468–474 (2006).
- Chapin, F. S. III et al. Consequences of changing biodiversity. *Nature* 405, 234–242 (2000).
- Clark, J. S. Uncertainty and variability in demography and population growth: A hierarchical approach. *Ecology* 84, 1370–1381 (2003).

Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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METHODS

Data selection. We used data from 228 North American Breeding Bird Survey (BBS)⁸ routes across ten states (Massachusetts, Connecticut, New Jersey, New York, Pennsylvania, Maryland, Virginia, Illinois, Colorado, Oregon) that represent WNV dispersal westward from the 1999 east coast introduction. We included routes that had at least 80% coverage from 1980 to 2005, and a maximum of two missing observations in years after WNV emergence. We selected 20 widespread and common North American bird species according to six criteria: (1) native to North America; (2) distribution includes New England/Mid-Atlantic states where WNV has been present the longest; (3) were regularly detected on BBS routes and in sufficient numbers along secondary roads, given habitat expectation and data; (4) breeding and vocalization season overlap with timing of BBS collection; (5) species for which some background information on susceptibility to WNV infection was available (Supplementary Table 1); and (6) chose species pool to cover the range of expected WNV impact. Finally, we randomly selected five additional species from the group that satisfied criteria 1–4 but that had not been studied in WNV infection experiments. This produced a total of 20 species, which was chosen as the number that we could efficiently model and evaluate.

Model. Our modelling goal was to propagate stochasticity and trend associated with two decades of avian population data before WNV arrival to construct probability distributions for expected abundance in years after WNV emergence.

We fit an overdispersed, Poisson regression model for counts at each route-by-year node where stochastic relationships among routes and observers were normally distributed random variables with mean zero and unknown variance²⁸. For a given species, individual counts, c_{jt} , were conditionally Poisson

$$c_{jt} \approx \text{Pois}(\lambda_{jt}) \quad j = 1, \dots, m; t = t, \dots, T \quad (1)$$

where subscripts j and t refer to route and year, respectively.

The expected value λ_{jt} for a given annual count was

$$\log(\lambda_{jt}) = \beta_k(t - t^*) + \kappa_k + \Phi_j + \Omega_{jt} + \varepsilon_{jt} \quad (2)$$

where β_k is the linear trend centred at mean year t^* over all routes in region k , Φ and Ω are random effects for variation among routes and observers respectively, and ε_{jt} are normally distributed error terms with mean zero. We evaluated each species' model individually for inclusion of region-specific inter-annual climate covariates κ (El Niño/Southern Oscillation (ENSO) index and North Atlantic Oscillation (NAO) evaluated in Supplementary Information) for reduced deviance information criterion²⁹ (DIC) values over a model with no inter-annual climate covariate. Model predictive ability was improved by including an annual ENSO effect for blue jay, chickadee, downy woodpecker, eastern towhee, gray catbird, mourning dove, song sparrow and tufted titmouse populations. Delineation of geographical regions (k) was also identified by DIC model comparison and fell generally along separation by state (except in the northeast where Pennsylvania, New York, New Jersey, Massachusetts and Connecticut were aggregated). We used standard vague priors on all unknown parameters. Hyperprior distributions for precision parameters were given inverse gamma distributions with mean 1 and variance 1,000. Models were fit by Gibbs sampler using the WinBUGS program²⁹. All models were run for 50,000 iterations following a 10,000 to 15,000 iteration 'burn-in'. Convergence was assessed through visual inspection and Gelman–Rubin diagnostics²⁹ on multiple Markov chains.

Of the total 5,928 route-by-year nodes, 576 were missing in the raw data. These missing data were scattered throughout the 228 routes but occurred disproportionately in the early part of the time series (most often between 1980 and 1987). We fit the model to BBS data and used the Gibbs sampler to adjust for differences among observers (skill and effort levels) and to estimate probability distributions for abundance in years and routes with missing observations. We fit the model to the 26-yr data set to create a replicate and complete time series for each route. We used a cross-validation procedure³⁰ that randomly removed 30% of the data and evaluated the model's ability to estimate these missing nodes. Correlation coefficients comparing observed and estimated nodes (given model presented) ranged between 0.68 and 0.98 among fits for individual species.

Predicted abundance estimates. We fit the model described above to data collected before WNV emergence only, and then estimated expected abundances at each route location in all subsequent years (that is, from 1999 for east coast, 2001 for Illinois, 2002 for Colorado and 2004 for Oregon¹¹). We directly compared the posterior probability distributions of expected abundances in post-WNV years with the true observations. We assigned significance to years where observed abundances fell outside 95% posterior credible intervals (95% CIs). If WNV emergence did not cause detectable mortality rates then we would expect no significant deviation between observed abundance and posterior predicted

abundance estimates (Supplementary Fig. 2).

28. Link, W. A. & Sauer, J. R. A hierarchical analysis of population change with application to Cerulean Warblers. *Ecology* **83**, 2832–2840 (2002).
29. Spiegelhalter, D. J., Best, N. G., Carlin, B. P. & van der Linde, A. d. Bayesian measures of model complexity and fit (with discussion). *J. Roy. Stat. Soc. B.* **64**, 583–640 (2002).
30. Gelfand, A. E. in *Markov Chain Monte Carlo in Practice* (eds Gilks, W. R., Spiegelhalter, D. J. & Richardson, S.) 145–158 (Chapman and Hall, London, 2006).