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Fine-Scale Variation in Vector Host Use and Force of Infection Drive Localized Patterns of West Nile Virus Transmission

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Abstract

The influence of host diversity on multi-host pathogen transmission and persistence can be confounded by the large number of species and biological interactions that can characterize many transmission systems. For vector-borne pathogens, the composition of host communities has been hypothesized to affect transmission; however, the specific characteristics of host communities that affect transmission remain largely unknown. We tested the hypothesis that vector host use and force of infection (i.e., the summed number of infectious mosquitoes resulting from feeding upon each vertebrate host within a community of hosts), and not simply host diversity or richness, determine local infection rates of West Nile virus (WNV) in mosquito vectors. In suburban Chicago, Illinois, USA, we estimated community force of infection for West Nile virus using data on Culex pipiens mosquito host selection and WNV vertebrate reservoir competence for each host species in multiple residential and semi-natural study sites. We found host community force of infection interacted with avian diversity to influence WNV infection in Culex mosquitoes across the study area. Two avian species, the American robin (Turdus migratorius) and the house sparrow (Passer domesticus), produced 95.8% of the infectious Culex spp. mosquitoes and showed a significant positive association with WNV infection in Culex spp. mosquitoes. Therefore, indices of community structure, such as species diversity or richness, may not be reliable indicators of transmission risk at fine spatial scales in vector-borne disease systems. Rather, robust assessment of local transmission risk should incorporate heterogeneity in vector host feeding and variation in vertebrate reservoir competence at the spatial scale of vector-host interaction.

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Introduction

Host community composition can exert a strong effect on vector-borne pathogen transmission when vertebrate reservoir competence varies among host community members [1,2,3,4,5]. Early studies of the relationship between host community structure and human disease [6] led to the proposal of ‘zooprophylaxis,’ where co-occurring vertebrate species may diminish the risk of vector transmitted diseases for a focal species, particularly humans [7,8]. Mechanistically, the process involves the ‘diversion’ or ‘wasting’ of vector feeding effort towards less-competent hosts and away from humans or more-competent hosts [2,9,10]. Recently, this argument has been recast as a ‘dilution effect’ [3], whereby host diversity itself reduces the risk of disease transmission. The appeal of ‘zooprophylaxis’ or the ‘dilution effect’ as a general principle derives from its focus on biodiversity as a barrier to vector-borne zoonotic disease transmission [11,12,13]. However, considering only diversity or richness as a measure of host community structure ignores ecological complexities inherent to any host-vector system, such as heterogeneities in vector host selection and variation in vertebrate reservoir competence.

The introduction and establishment of West Nile virus (WNV) into North America [14] offers an opportunity to explore associations between host community composition and arbovirus transmission. WNV is maintained in an enzootic transmission cycle by Culex spp. mosquitoes, principally Culex pipiens in the eastern United States north of 36° latitude [13,16,17], and a suite of bird species that vary in their competence [18,19]. Previous studies have reported inverse associations between non-passerine bird species richness and human WNV cases [20], and between WNV infection in Culex mosquitoes and the percent of wetland cover [21], as well as positive associations between high avian diversity and low WNV incidence in humans in the eastern United States [22]. Allan et al [23] found that WNV infection in
mosquitoes and incidence in humans increased with decreasing bird diversity and increasing vertebrate reservoir competence of the bird community, while Koenig et al. [24] found that the decline of the American crow (Corvus brachyrhynchos) was accelerated in areas of low avian diversity. Although all of these studies suggest a pattern in which increased host diversity or richness dampens WNV transmission, these studies have not accounted for host selection by vectors, a potentially critical determinant of pathogen transmission, given that vectors do not feed in proportion to host abundance [16,25,26,27].

Selective feeding by vectors in the case of WNV suggests that a small number of avian species (i.e., ‘super-spreaders’) might be responsible for the majority of WNV transmission [16,28], even when avian community diversity is high. Further, non-random host selection by mosquitoes modifies the effect of vertebrate reservoir competence on the prevalence of WNV in vectors [19,25]. Described as heterogeneities in the host community, non-random host selection has been observed in other disease systems [29,30,31], with results suggesting nonlinear effects on pathogen transmission. The processes of host-selection, and more broadly host-vector contact, operate on a very fine spatial scale; therefore, analysis of these relationships at coarser scales (e.g., county or region) could easily obscure important local patterns that affect pathogen transmission more directly [32].

To test the hypothesis that attributes of the host community such as vertebrate reservoir competence and selection by arthropod vectors may be more accurate predictors of arboviral transmission than vertebrate host diversity or richness, we characterize the WNV transmission cycle at a fine spatial scale within an urban focus of infection in Chicago, USA. In particular, we focus on “host community force of infection”, defined here as the summed number of infectious mosquitoes resulting from each vertebrate host upon which vectors feed. This quantity incorporates empirical measures of mosquito host selection derived from blood meal analyses of mosquitoes and indices of vertebrate reservoir competence. We focus on Culex mosquitoes, the primary vectors of WNV in North America, because host selection is known to vary across North America for this vector [26,28]. We compare fine-scale Culex feeding patterns in relation to bird communities surveyed at the same sites. Finally, we model several characteristics of the host community, including community force of infection, avian diversity, and richness as predictors of WNV infection in Culex mosquitoes.

Materials and Methods

Study area and sampling

The study region in southwest Chicago, Illinois (Cook County; 87°44’ W, 41°42’ N) consisted of 26 different residential sites and five “semi-natural sites” (three cemeteries, one wildlife refuge, and one forest preserve). Permission to conduct this research was obtained from the Villages of Alsip, Evergreen Park, Indian Head Park, Oak Lawn, Palos Hills, Western Springs, the City of Blue Island, Burbank, Chicago, Harvey, the Archdiocese of Chicago, and many private homeowners within these municipalities. Residential sites were selected to represent a range of human population densities and distances to semi-natural areas, as previously described [33,34]. To estimate mosquito abundance and infection, we deployed CDC light and gravid traps from mid-May to mid-October in 2005–2008; after species identification, we pooled individuals according to species, location of collection, and blood-feeding status (fed or non-fed; details in Methods S1). We used quantitative real-time polymerase chain reaction (qRT-PCR) to detect WNV and estimated the annual per-site Culex spp. mosquito infection rate according to the maximum likelihood method [35]. In addition, we estimated the relative abundance of Culex spp. mosquitoes (number per light trap night) to control for vector density effects which are known to influence relationships between host communities and disease risk [36]. We used the blood-fed Culex pipiens for molecular identification of vertebrate blood meal source (see Methods S1). We surveyed bird communities in 2006 using point counts [34] and estimated bird densities using the program Distance 5.0 [37].

Host selection. Host feeding selection for birds was estimated using the Manly resource selection design II index [38], a ratio that uses relative density as the measure of host availability (density-based selection ratio; \( w_i \)) and was estimated for Cx. pipiens at follows:

\[
\hat{w}_i = \frac{\text{proportion of utilized bird species } i}{\text{proportion of available bird species } i}
\]

The Manly selection ratio equals 1 when mosquito feeding on host \( i \) is in equal proportion to estimated availability; is > 1 when a host is overused (i.e., more frequent feeding than expected by chance), and is < 1 when a host is underused (i.e., less frequent feeding than expected by chance). The selection index and standard error were calculated using the adehabitat package in Program R [39]. We collected Culex pipiens blood-feeding data at 23 study sites that also had bird survey data, for the purpose of this study, and in order to maintain statistical power, we present results for sites with at least 18 avian-derived blood meals (\( n = 11 \) sites). Over- or under-utilization of a host species was considered statistically significant when the 95% confidence interval did not overlap unity.

When estimating the Manly host selection ratio, bird species that were not observed as blood meal hosts but were identified in bird surveys were given a blood meal value of one. Bird species observed as blood meal hosts but not observed in bird surveys were given a density equal to the lowest observed bird density at each site. Host selection values were aggregated by site across years, since sample sizes in some years at some sites were too low for meaningful statistical analysis.

Force of infection

For each of the sites, we estimated the number of infectious Cx. pipiens mosquitoes \( (F_i) \) resulting from vector feeding on each host according to \( F_i = B_i^2 C_i \) [26], where \( B_i \) equals the fraction of the total blood meals from host \( i \) and \( C_i \) equals the vertebrate reservoir competence index [18]. Bird species without a competence index were assigned the average competence value for their respective taxonomic family [18]. For several species, family-level competence values were not available, so the average competence for the respective avian order was assigned (Passeriform = 0.773; Charadriiform = 1.018). The competence for all mammalian hosts was zero except for gray squirrel (Sciurus carolinensis) \( (C_i = 0.066; \) [40]). The force of infection assumes equal initial seroprevalence among hosts and equal feeding rates and competence values for adult and juvenile birds.

To characterize community-wide force of infection, we used the sum of \( F_i \) for each study site. Originally, force of infection described the per capita rate at which a susceptible individual acquires infection [41]. In a system with multiple species of hosts, the expression represents the total force of infection exerted at all host species in a community [1]. We report community force of infection for sites with at least 20 identified Cx. pipiens blood meals (data aggregated among years) but for the modeling described
below, we calculated community force of infection for sites within years.

**Statistical analysis**

To explore associations between *Cx. pipiens* blood feeding patterns and local avian diversity measures, we compared diversity index values and richness for blood meal data and bird survey data at the same sites. Estimated species diversity was derived using the Shannon index, which incorporates both species richness and evenness [42]. In calculating the diversity of blood meal data, we aggregated data across 4 years to maintain statistical power and only included 16 sites in the analysis that had at least 10 identified avian *Cx. pipiens* blood meals (493 blood meals distributed among 16 sites). We used paired *t*-tests to evaluate the associations of avian diversity and richness and blood meal diversity and richness among the sites.

For the initial modeling effort, we used linear mixed effects models to examine relationships among *Culex* spp. infection rate, attributes of the host community (community force of infection, avian diversity, avian richness), and vector abundance (number of *Culex* spp. per light trap night). Sites and years were included as random factors and the significance of the fixed factors was estimated with a parametric bootstrap [43]. We included weights to account for unequal variance and unequal numbers of observations in estimating the fraction of total blood meals from host *i*. Specifically, weights were proportional to the number of blood-fed mosquitoes collected among sites. Candidate models included all combinations of these variables, including single-variable models [44].

For the subsequent modeling effort, we used general linear models to investigate the relationship between force of infection for each bird species ($B_i^2 \times C_i$) and *Culex* infection rate. This second modeling effort did not include site and year as random effects because previously fitted linear mixed effects models revealed those factors to have zero variance. Candidate models included force of infection for avian species that were abundant or commonly fed upon ([American robin (*Turdus migratorius*), house finch (*Carpodacus mexicanus*), house sparrow (*Passer domesticus*), mourning dove (*Zenaida macroura*), northern cardinal (*Cardinalis cardinalis*), and European starling (*Sturnus vulgaris*). To determine the sensitivity of sample size on the results of the models, we created separate statistical models using data for sites with at least 8, 10, and 15 identified *Cx. pipiens* blood meals per year (resulting in sample sizes of 27, 21, 14, respectively). The results of the models for the different datasets with different sample size cut-offs were similar and results are presented for the cut-off of 10. We used the Akaike Information Criterion with a bias correction term for small samples size (AICc) to evaluate candidate models [44]. Residuals from models were inspected with diagnostic plots to ensure that model assumptions were met (see Figure S1). All tests were computed in R v2.11.1 statistical programming language [39].

**Results**

**Mosquito collection**

Between 2005 and 2008, we collected 2,971 *Culex* spp. pools, totaling 57,053 individuals. Infection rates for each year and site ranged from 9.8 per 1,000 (C.I. = 5.2–17.1) to 30.7 per 1,000 (C.I. = 17.0–52.9) for the 14 sites with host community force of infection data (Fig. 1). The average number of *Culex* spp., mosquitoes captured per light trap night within years (early-Jul.

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**Figure 1. Map of study sites in suburban Chicago, Illinois, U.S.A.** Site names are as follows: Oak Lawn - North (3), Oak Lawn - Central (5), Evergreen Park - West (7), Blue Island (9), Chicago - Ashburn East (10), Alsip (11), Burbank (12), Indian Head Park (15), Western Springs (16), Harvey (19), Holy Sepulchre Cemetery (HS), Saint Casimir’s Cemetery (SC), Evergreen Cemetery (EC), Wolfe Wildlife Refuge (WW). doi:10.1371/journal.pone.0023767.g001
to late-Sept.) ranged from 0.8 to 60.3 (mean of 16.4 and median of 10.8).

**Culex pipiens** host selection, avian community structure, and force of infection

We collected 1,614 blood-fed mosquitoes, and of the *Culex* spp. mosquitoes collected, 869 were *Cx. pipiens* (64.9%), 256 were *Cx. restuans* (19.1%), 2 were *Cx. salinarius* (0.1%). A total of 213 *Culex* mosquitoes (15.9%) could not be identified using our PCR-based methods. We obtained blood meal identifications for 1,085 of the total individuals (67.2%) and 652 of the *Cx. pipiens* (75.0%). The over- or under-utilization of each host species by *Cx. pipiens* was not consistent among sites (Table S1).

We found that the diversity of hosts fed upon by *Cx. pipiens*, as determined by blood meal analysis, was significantly different from avian diversity at the same site (*t* = -2.78, d.f. = 15, *P* = 0.014) and that blood meal richness was significantly different from avian richness (*t* = -5.73, d.f. = 15, *P* < 0.001). Sites with high avian diversity based on point count surveys did not have high diversity of birds that were fed upon by *Cx. pipiens*. Birds surveyed at high diversity sites such as SC and WW (both urban green spaces) that were not represented in the 652 blood meals from the study region included American crow, brown-headed cowbird (*Molothrus ater*), black-crowned night-heron (*Nycticorax nycticorax*), Canada goose (*Branta canadensis*), common yellowthroat (*Geothlypis trichas*), downy woodpecker (*Picoides pubescens*), eastern kingbird (*Tyrannus tyrannus*), eastern meadowlark (*Sturnella magna*), great blue heron (*Ardea herodias*), mallard (*Anas platyrhynchos*), monk parakeet (*Myiopsitta monachus*), red-eyed vireo (*Vireo olivaceus*), ring-necked pheasant (*Phasianus colchicus*), warbling vireo (*Vireo gilvus*), willow flycatcher (*Empidonax traillii*), and yellow warbler (*Dendroica petechia*).

The aggregate force of infection for all sites and years combined demonstrated the American robin to rank highest, accounting for 86.7% of the total force of infection, followed by house sparrow (9.1%) and house finch (2.1%; Table S2).

**Modeling host community structure and *Culex* infection rate**

Host community force of infection for each site ranged from 0.05 to 0.73 (mean of 0.21±0.04; Fig. 2A). To investigate the influence of host community structure on *Culex* infection rate, a model selection procedure indicated that the data were best fit by a model (lowest AICc value and highest weight) that included an interaction term of community force of infection and diversity (Fig. 3; Table 1; parameter ± S.E. = -101.63±3.35, 95% bootstrap confidence intervals = -127.05 to -75.10, *P* = 0.036).

Figure 2. Scatterplots showing relationships between *Culex* spp. mosquito infection rate (# positive per 1,000) and host community force of infection and avian diversity (Shannon index) (A), and American robin and house sparrow force of infection (B), in study sites in southwest suburban Chicago, Illinois, U.S.A., 2005-2008. Symbols represent year (circle = 2005, triangle = 2006, cross = 2007), and labels are the site identification code.

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The main effects of this model were not significant (community force of infection parameter = 188.58±5.48, \( P = 0.179 \); avian diversity parameter = 12.65, \( P = 0.086 \)).

We further explored the relationship between the force of infection \( (B_i^2 * C_i) \) for individual bird species and Culex infection rate. The linear models did not include random factors of year and site due to the lack of variation explained by those factors. A model selection process including all combinations of variables resulted in 54 competing models and the best model (lowest AICc) included the force of infection for American robin, house sparrow, and European starling (Table 2 and Fig. 2B; AICc = 140.1, \( F = 3.27, r^2 = 0.25, d.f. = 3 \) and 17, and \( P = 0.047 \)). The second best model explaining variation in Culex infection rate included American robin and house sparrow force of infection (AICc = 140.5, \( F = 3.22, r^2 = 0.18, d.f. = 2 \) and 18, and \( P = 0.064 \)).

**Discussion**

*Culex* infection rate was best explained by a model including the interaction of host community force of infection and host diversity. Specifically, the interaction of community force of infection and avian diversity yielded a significant nonlinear relationship as predictors of the prevalence of virus infection in the vector mosquito population. This interaction implies that increases in avian diversity do not result in a concomitant linear increase or decrease in *Culex* infection rate. Rather, the direction of change in the host diversity and infection interaction depends upon parallel changes in host selection and the reservoir competence of those hosts. Sites with moderate levels of avian diversity tended to have higher host community force of infection. This interaction is similar to the interaction of landscape features on mosquito species richness at the same study sites, where the most heterogeneous landscapes harbored the largest number of species [45]. Importantly, the models that included force of infection had higher explanatory power than models including only avian richness or diversity. Moreover, force of infection from two species, the American robin and the house sparrow, were significant predictors of WNV infection in *Culex* spp. mosquitoes.

When estimating the proportional contribution of each avian species to WNV transmission, our model incorporated birds utilized as hosts by arthropod vectors and did not rely on birds that were only surveyed during point counts. As a result, our model was able to account indirectly for several avian functional traits that lead to non-random host selection, thereby producing a metric of community force of infection that would not have been attainable otherwise. By indirectly modeling traits such as avian body mass, roosting habitat, and anti-mosquito behavior alongside mosquito functional traits such as host location [46], we were able to calculate a biologically realistic index of the risk of WNV transmission. In this sense, our analysis is similar to measures of “functional diversity” that describe organismal traits that influence ecosystem function and productivity [47,48].

Our results show that certain members of the avian community have disproportionate contributions to amplification and transmission of WNV. This result, in turn, demonstrates that avian diversity and richness as measured by point counts are uncoupled from the diversity and richness of birds utilized as hosts by *Cx. pipiens* at the same sites. We also show that 16 avian species detected by bird
surveys were not identified in *Cx. pipiens* blood meals from the same sites, despite extensive sampling. In a recent study, McKenzie and Goulet [49] considered non-random host selection and variation in vertebrate reservoir competence to WNV when evaluating the influence of the host community composition to WNV disease risk. Their study suggested that a small component of the bird community, characterized by species with high amplification fractions [16], were significant predictors of human WNV cases in Colorado, USA. Taken together, these results demonstrate that the mere presence of a species in a community of potential hosts does not necessarily merit its inclusion as a contributor to the force of infection of the vector population.

Our current and previous results [16] provide a spatially detailed description of *Cx. pipiens* host selection. When calculating host selection among sites at a fine spatial scale, we show that the over-utilization of robins is not always consistent among sites. For example, at site SC (Saint Casimir’s cemetery), robins were significantly under-utilized, meaning that they were used less than would be expected based on availability, which is contrary to the selection index for robins observed in previous studies [16,26,28]. One explanation for this pattern is that the bird communities surveyed during the day do not necessarily reflect the roosting birds available to mosquitoes at night. During ongoing research, we observed that radio-tagged robins that are present in this cemetery during the day primarily roost outside the cemetery at a large communal roost, which implies that these robins are unavailable to night-time host-seeking mosquitoes in this cemetery.

Calculating the force of infection for individual species at each site, and for the study area as a whole identified American robins as having the highest force of infection (0.160), followed by house sparrow (0.017), house finch (0.004), and northern cardinal (0.002). These results highlight that American robin and house sparrow produced 95.8% of the infectious *Cx. pipiens* mosquitoes and were positively associated with WNV infection in *Culex* mosquitoes. These results support the broad importance of American robins as WNV amplification hosts [16,26,28], and offer new data in support of the contribution of house sparrows and house finches to WNV transmission [26,50].

One assumption of this study is that avian host behavior is not detrimental to mosquito survival. Mortality risk from predation by vertebrate hosts has been observed in the field [51,52], and simulation modeling has demonstrated a trade-off between feeding persistence of mosquitoes [53] and the rate at which vectors die while searching for a blood meal [54]. A recent empirical study identified 9% mortality in *Cx. pipiens* mosquitoes that attempted to feed on house sparrows or chickens [55]. Keesing et al. [56] recently evaluated how host community composition could affect tick survival and found that some hosts can kill thousands of ticks per hectare. These hosts act as “ecological traps” [57], and resulted in an estimated 82.8% to 96.5% mortality in larval *Ixodes scapularis* ticks. This rate of host-related vector mortality is probably much greater in ticks than mosquitoes; however, more data evaluating interspecific variation in mosquito predation is warranted.

This study takes the novel approach of incorporating host community force of infection as a key variable for explaining fine scale variation in transmission of a multi-host mosquito-borne pathogen. We observed a relationship between *Culex* infection rate and the interaction of host community force of infection and avian diversity; this pattern was driven by virus amplification in two bird species, the American robin and house sparrow. Ideally, future studies would focus on providing insights into the processes that explain the relationships between host community force of infection and disease risk, and on the ultimate goal of informing a general model for WNV occurrence across spatial scales. Taken together, our results suggest that the influence of host community structure on vector-borne disease risk is conditional and influenced by heterogeneity in vector-host contact and variation in competence within the vertebrate reservoir community.

**Supporting Information**

**Methods S1** This file includes additional methodological descriptions regarding mosquito collection, laboratory diagnostics, and avian host surveys.

**Figure S1** This file contains the diagnostic plots (residuals and Q-Q plot) for the statistical models.

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**Table 1.** Candidate models for predicting *Culex* infection rate with site and year included as random effects in the linear mixed effect model with unequal variance.

| Model                  | AICc  | ΔAICc | wi   |
|------------------------|-------|-------|------|
| FOI*Div                | 181.2 | 0.0   | 0.5851 |
| FOI+Div+FOI*Div        | 183.8 | 2.6   | 0.1604 |
| FOI*Rich+Div           | 183.9 | 2.7   | 0.1526 |
| FOI*Rich               | 185.3 | 4.1   | 0.0758 |
| FOI*Rich+Div+CxDen     | 188.3 | 7.1   | 0.0168 |
| FOI*Div+Rich+CxDen     | 190.4 | 9.2   | 0.0059 |
| FOI*Rich+Div+CxDen     | 192.5 | 11.3  | 0.0021 |
| CxDen+FOI*Rich         | 195.2 | 14.0  | 0.0005 |
| FOI+Div                | 195.6 | 14.4  | 0.0004 |
| FOI+CxDen+Div          | 198.2 | 17.0  | 0.0001 |
| FOI+CxDen              | 200.6 | 19.4  | 0.0000 |
| FOI+CxDen+Div+Rich     | 200.7 | 19.5  | 0.0000 |
| FOI+Rich               | 201.6 | 20.4  | 0.0000 |
| FOI+CxDen              | 202.9 | 21.7  | 0.0000 |
| Div                    | 203.7 | 22.5  | 0.0000 |
| Rich+FOI*CxDen         | 203.9 | 22.7  | 0.0000 |
| FOI+Div+Rich+CxDen     | 204.2 | 23.0  | 0.0000 |
| Rich                   | 208.9 | 27.7  | 0.0000 |
| CxDen                  | 210.5 | 29.3  | 0.0000 |

FOI = community force of infection; Div = avian diversity; Rich = avian richness; CxDen = *Culex* captured per light trap night.

**Table 2.** Model parameters for the top ranked model utilizing individual bird force of infection to predict the *Culex* infection rate in suburban Chicago, 2005-2007.

| Variable                          | Estimate S.E. | t-value | P-value |
|-----------------------------------|---------------|---------|---------|
| American robin force of infection | 12.12         | 4.48    | 2.71    | 0.015   |
| House sparrow force of infection  | 63.18         | 34.66   | 1.82    | 0.086   |
| European starling force of infection | 1797.98      | 1084.51 | 1.66    | 0.116   |

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Table S1  This file is a table of Cx. pipiens host selection ratios for each host species at 11 field sites in southwest suburban Chicago, Illinois. (DOC)

Table S2  This file contains host species force of infection values which represent the number of infectious Cx. pipiens mosquitoes resulting from feeding on each host species. (DOC)

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Author Contributions

Conceived and designed the experiments: GLH UDK JDB MOR EDW TLG. Performed the experiments: GLH SRL. Analyzed the data: GLH LFC. Contributed reagents/materials/analysis tools: EDW. Wrote the paper: GLH LFC TKA.

References

1. Dobson A (2004) Population dynamics of pathogens with multiple host species. Am Nat 164: 364–378.
2. Norman R, Bowers RG, Bogen M, Hudson PJ (1999) Persistence of tick-borne virus in the presence of multiple host species: Tick reservoirs and parasite mediated competition. J Theor Biol 200: 111–118.
3. Ostfeld RS, Keesing F (2000) The function of biodiversity in the ecology of vector-borne zoonotic diseases. Can J Zool 78: 2061–2078.
4. Power AG, Mitchell CE (2004) Pathogen spill-over in disease epidemics. Am Nat 164: 579–589.
5. Chaves LF, Hernandez MJ, Dobson AP, Pascual M (2007) Sources and sinks: revisiting the criteria for identifying reservoirs for American cutaneous leishmaniasis. Trends Parasit 23: 311–316.
6. Celi A (1933) The history of malaria in the Roman Campagna from ancient times. London: John Bale, Sons Danielson, ltd.
7. Sota T, Mogi M (1989) Effectiveness of zoonoprophylaxis in malaria control - a theoretical inquiry with model for mosquito populations with two bloodmeal hosts. Med Vet Entomol 3: 337–345.
8. Service MW (1991) Agricultural-development and arthropod-borne diseases- a review. Rev Suda Publ 25: 163–178.
9. Telfer S, Bowen KJ, Sekules R, Bogen I, Hayden T, et al. (2005) Disruption of a host-parasite system following the introduction of an exotic host species. Parasitol 130: 661–668.
10. Keesing F, Holt RD, Ostfeld RS (2006) Effects of species diversity on disease risk. Ecology Letters 9: 485–496.
11. Pongiri MJ, Roman J, Ezenwa VO, Goldberg TL, Koren HS, et al. (2009) Biodiversity loss affects global disease ecology. Bioscience 59: 945–954.
12. Ashgil RMN (2010) Deformation and avian infectious diseases. J Exp Biol 213: 955–960.
13. Keesing F, Ebeling LK, Daszak P, Dobson A, Harvell CD, et al. (2010) Impacts of biodiversity on the emergence and transmission of infectious diseases. Nature 468: 647–652.
14. Weaver SC, Reisen WK (2010) Present and future arboviral threats. Antiviral Res 85: 328–345.
15. Andreadis TG, Anderson JF, Vosbrinck CR, Main AJ (2004) Epidemiology of West Nile virus in Connecticut: A five-year analysis of mosquito data 1999-2003. Vector-Borne Zoonotic Dis 4: 360–378.
16. Hamer GL, Kitron UD, Goldberg TL, Brawn JD, Loss SR, et al. (2009) Host selection by Culex pipiens mosquitoes and West Nile virus amplification. Am J Trop Med Hyg 80: 260–278.
17. Turell MJ, Dohn DJ, Sardelas MR, O Guinn ML, Andreadis TG, et al. (2005) An update on the potential of North American mosquitoes (Diptera: Culicidae) to transmit West Nile virus. J Med Entomol 42: 57–62.
18. Kilpatrick AM, LaDeau SL, Marra PA (2007) Ecology of west Nile virus and its impact on birds in the western hemisphere. Anu 124: 1121–1136.
19. Komar N, Langevin S, Hinten S, Nemeth N, Edwards E, et al. (2003) Experimental infection of North American birds with the New York 1999 strain of West Nile virus. Emerg Infect Dis 9: 311–322.
20. Ezenwa VO, Godsey MS, King RJ, Guptrill SC (2006) Avian diversity and West Nile virus: testing associations between biodiversity and infectious disease risk. Proc R Soc B Biol Sci 273: 109–117.
21. Ezenwa VO, Millheim LE, Coffey MF, Godsey MS, King RJ, et al. (2007) Land cover variation and West Nile virus prevalence: patterns, processes, and implications for disease control. Vector-Borne Zoonotic Dis 7: 173–180.
22. Swaddle JP, Gales SF (2008) Increased avian diversity is associated with lower incidence of human West Nile infection: observation of the dilution effect. PLoS ONE 3.
23. Allan BF, Langerhans RB, Ryberg WA, Landesman WJ, Griffin NW, et al. (2009) Ecological correlates of risk and incidence of West Nile virus in the United States. Oecologia 163: 899–908.
24. Koening WD, Hochachka WM, Zuckerberg B, Dickinson JL (2010) Ecological determinants of American crow mortality due to West Nile virus during its North American sweep. Oecologia 163: 903–909.
25. Chaves LF, Harrington LC, Krieg CL, Nguyen AM, Kitron UD (2010) Blood host community structure of mosquitoes: random or structured? Front of Zool 7.
26. Kent R, Juliusson L, Weismann M, Evans S, Komar N (2009) Seasonal Blood-Feeding Behavior of Culex tarsalis (Diptera: Culicidae) in Weld County, Colorado, 2007. J Med Entomol 46: 380–390.
27. Lyimo IN, Ferguson HM (2009) Ecological and evolutionary determinants of host species choice in mosquito vectors. Trends Parasitol 25: 189–196.
28. Kilpatrick AM, Daszak P, Jones MJ, Marra PP, Kramer LD (2006) Host heterogeneity dominates West Nile virus transmission. Proc R Soc B Biol Sci 273: 2327–2333.
29. Brison D, Dykhuizen DE, Ostfeld RS (2008) Conspicuous impacts of inconspicuous hosts on the Lyme disease epidemic. Proc R Soc B Biol Sci 275: 227–235.
30. Dye C, Hasibeder G (1986) Population-dynamics of mosquito-borne disease - effects of flies which bite some people more frequently than others. Trans R Soc Trop Med Hyg 80: 69–77.
31. Woolhouse MEJ, Dye C, Earn JD, Smith T, Charlwood JD, et al. (1997) Heterogeneities in the transmission of infectious agents: Implications for the design of control programs. Proc Natl Acad Sci U S A 94: 338–342.
32. Eisen L, Eisen RJ (2007) Need for improved methods to collect and present spatial epidemiologic data for vectorborne diseases. Emerg Infect Dis 13: 1816–1820.
33. Hamer GL, Walker ED, Brawn JD, Loss SR, Ruiz MO, et al. (2008) Rapid amplification of West Nile virus: the role of hatch-year birds. Vector-Borne Zoonotic Dis 8: 57–67.
34. Loss SR, Hamer GL, Walker ED, Ruiz MO, Goldberg TL, et al. (2009) Avian host community structure and prevalence of West Nile virus in Chicago, Illinois. Oecologia 159: 415–424.
35. Biggerstaff B (2006) PooldinRate, Version 3.0: a Microsoft Excel Add-In to compute prevalence estimates from pooled samples. Centers for Disease Control and Prevention, Fort Collins, CO.
36. Bogen M (2008) Effects of host diversity on disease dynamics. In: Ostfeld RS, Keesing F, Evnier VT, eds. Infectious Disease Ecology: Effects of Ecosystems on Disease and of Disease on Ecosystems. Princeton, NJ: Princeton University Press pp 12–29.
37. Thomas L, Buckland ST, Rexstad EA, Laake JL, Strindberg S, et al. (2010) Distance software: design and analysis of distance sampling surveys for estimating population size. J Appl Ecol 47: 5–14.
38. Manly BF, McDonald DL, McDonald TL, McDonald R, Erickson WP (2002) Resource Selection by Animals: Statistical Design and Analysis for Field Studies. Dordrecht, Netherlands: Kluwer Academic Publishers. 221 p.
39. R Development Core Team (2008) R: A language and environment for statistical computing. Vienna/Austria. R Foundation for Statistical Computing.
40. Platt KB, Tucker BJ, Halbur PG, Blenkins B, Fabiosa FG, et al. (2006) Fox squirrels (Sciurus niger) develop West Nile virus viremias sufficient for infecting select mosquito species. Vector-Borne Zoonotic Dis 6: 225–233.
41. Anderson RM, May RM, eds (1991) Infectious Diseases of Humans. New York: Oxford University Press Inc. 757 p.
42. Maguran AE (2004) Measuring Biological Diversity. Oxford: Blackwell Publishing. 260 p.
43. Chaves LF (2010) An entomologist guide to demystify pseudoreplication: data analysis of field studies with design constraints. J Med Entomol 47: 291–298.
44. Burnham KP, Anderson DR (2002) Model selection and inference: a practical information-theoretic approach. New York: Springer-Verlag.
45. Simpson JE, Folsom-O’Keefe CM, Childs JE, Simons LE, Andreadis TG, et al. (2010) Need for improved methods to collect and present spatial epidemiologic data for vectorborne diseases. Emerg Infect Dis 13: 1816–1820.
46. Plackett RL, McDonald DL, McDonald TL, McDonald R, Erickson WP (2002) Resource Selection by Animals: Statistical Design and Analysis for Field Studies. Dordrecht, Netherlands: Kluwer Academic Publishers. 221 p.
47. R Development Core Team (2008) R: A language and environment for statistical computing. Vienna/Austria. R Foundation for Statistical Computing.
49. McKenzie VJ, Goulet NE (2010) Bird community composition linked to human West Nile virus cases along the Colorado Front Range. EcoHealth 7.

50. Darbro JM, Dhoundt AA, Vermeulen FM, Harrington LC (2007) Mycoplasma gallisepticum infection in house finches (Carpodacus mexicanus) affects mosquito blood feeding patterns. Am J Trop Med Hyg 77: 488–494.

51. Corbet PS, Downe AER (1966) Natural hosts of mosquitoes in northern ellesmere island. Arctic 19: 153–161.

52. Griffing SM, Kilpatrick AM, Clark L, Marra PP (2007) Mosquito landing rates on nesting American robins (Turdus migratorius). Vector-Borne Zoonotic Dis 7: 437–443.

53. Anderson RA, Roitberg BD (1999) Modelling trade-offs between mortality and fitness associated with persistent blood feeding by mosquitoes. Ecology Letters 2: 98–105.

54. Saul A (2003) Zooprophylaxis or zoopotentiation: the outcome of introducing animals on vector transmission is highly dependent on the mosquito mortality while searching. Malaria Journal 2.

55. Darbro JM, Harrington LC (2007) Avian defensive behavior and blood-feeding success of the West Nile vector mosquito, Culex pipiens. Behav Ecol 18: 750–757.

56. Keesing F, Brunner J, Duerr S, Killilea M, LoGiudice K, et al. (2009) Hosts as ecological traps for the vector of Lyme disease. Proc R Soc B Biol Sci 276: 3911–3919.

57. Robertson BA, Hutto RL (2006) A framework for understanding ecological traps and an evaluation of existing evidence. Ecology 87: 1075–1083.
METHODS S1 This file includes additional methodological descriptions regarding mosquito collection, laboratory diagnostics, and avian host surveys.

Mosquito collection, identification, and WNV infection rate

Mosquitoes were sampled from study sites once every two to three weeks from mid-May through mid-October in 2005—2008, using CO₂-baited CDC miniature light traps, CDC gravid traps baited with rabbit pellet infusion, and battery-powered backpack aspirators. The number of light traps and gravid traps deployed at each site was consistent within each year. Mosquitoes were identified to species morphologically [1] and blood-fed individuals were separated from gravid and unfed individuals. *Cx. pipiens* and *Cx. restuans* were pooled together during processing due to the difficulty in distinguishing the two based on morphological characteristics [2]. Non-blood-fed female mosquitoes were pooled into groups of 50 or less, by species, location of collection, and tested for WNV RNA using reverse transcription, real time polymerase chain reaction (PCR). Mosquitoes were homogenized by adding 1 mL of a 50:50 mixture of phosphate-buffered saline (PBS) and 2X lysis buffer (Applied Biosystems, Foster City, CA) and three #7 steel shots using a high-speed mechanical homogenizer (Retsch MM 300) for 4 minutes at 20 cycles/second. Each homogenized pool was centrifuged for 2 minutes at 13,000 rpm. RNA was extracted from mosquito pools using an ABI Prism 6100 Nucleic Acid Prep Station following the Tissue RNA Isolation Protocol (Applied Biosystems; P/N 4330252). RNA was eluted in a final volume of 60 μL of elution solution. A region of the WNV RNA envelope gene was detected using real-time, reverse transcription polymerase chain reaction (RT-PCR) [3]. The thermocycling was performed on an ABI Prism 9700HT sequence detector at the Research Technology Support Facility at Michigan State University, following the Taq-
Man One-Step RT-PCR Master Mix Protocol (Applied Biosystems; P/N 04310299). The amplification threshold was determined by serial dilutions of controls and a maximum cycle threshold for samples to be considered positive was 40. Mosquitoes were processed during the RNA extraction and RT-PCR on 96-well plates and each plate contained at least two positive extraction controls and an additional RT-PCR positive control. All plates had at least 10 negative controls (blanks) distributed evenly on the plate for quality control. Results were only accepted when positive and negative controls on each plate were clean and all positive field collected pools were confirmed by a second extraction and RT-PCR. Maximum likelihood estimates for infection rates were calculated using the Pooled Infection Rate version 3.0 Microsoft Excel add-in [4].

Spatial variation in disease risk at each site was estimated as the mean Culex spp. infection rate among years. Spatial variation in vector density was estimated as the number of Culex spp. mosquitoes captured per light trap night for each year. Only data from weeks 27 to 38 (early July to late September) were used to calculate Culex infection rates and Culex relative abundances; in doing so, trap sampling effort was standardized among years. Blood-fed Culex spp. mosquitoes were identified to species using a PCR based method and the remainder of the mosquito was tested for WNV.

**Mosquito blood meal analysis**

Following the methods described by Hamer et al. [5], DNA was extracted from the blood-fed abdomen of mosquitoes and a series of PCRs were used to amplify different regions of the cytochrome b gene of putative blood meal sources. PCR amplicons were visualized, purified, and sequenced directly on ABI 3730 Genetic Analyzer at the Research Technology Support Facility at Michigan State University. Sequences were queried against GenBank using
the BLAST algorithm to identify the closest match, which was assigned as the blood meal. Negative controls were carried through all steps, and 16 species of birds, 8 species of mammals, and 2 species of amphibians were correctly identified as positive controls.

**Host community surveys**

Local bird abundance was estimated at each site in 2006 using the point count method [6,7]. Five points were established in each of the twenty-one residential sites and eight points in each of the five natural sites. Surveys were conducted between 0.5 hour before sunrise and 4.0 hours after sunrise (0530-1000) on days with no precipitation and wind speed less than 24 km/hr. Two surveys were conducted between June and mid-July, corresponding to the peak of avian breeding in the region. Five-minute unlimited radius point counts were conducted at each survey point, distance to each observed bird was recorded, and density of each species and total avian density were estimated using Program DISTANCE 5.0 [8]. Relative abundance of individual species was calculated by dividing species density by total bird density.

**References**

1. Andreadis TG, Thomas MC, Shepard JJ (2005) Identification Guide to the Mosquitoes of Connecticut. New Haven, CT: The Connecticut Agricultural Experiment Station.
2. Harrington LC, Poulson RL (2008) Considerations for accurate identification of adult Culex restuans (Diptera : Culicidae) in field studies. J Med Entomol 45: 1-8.
3. Lanciotti RS, Kerst AJ, Nasci RS, Godsey MS, Mitchell CJ, et al. (2000) Rapid detection of West Nile virus from human clinical specimens, field-collected mosquitoes, and avian samples by a TaqMan reverse transcriptase-PCR assay. J Clin Microbiol 38: 4066-4071.
4. Biggerstaff BJ (2006) PooledInfRate, Version 3.0: a Microsoft Excel Add-In to compute prevalence estimates from pooled samples. Centers for Disease Control and Prevention. Fort Collins, CO.

5. Hamer GL, Kitron UD, Goldberg TL, Brawn JD, Loss SR, et al. (2009) Host selection by Culex pipiens mosquitoes and West Nile virus amplification. Am J Trop Med Hyg 80: 268-278.

6. Hutto RL, Pletschet SM, Hendricks P (1986) A fixed-radius point count method for nonbreeding and breeding-season use. Auk 103: 593-602.

7. Loss SR, Hamer GL, Walker ED, Ruiz MO, Goldberg TL, et al. (2009) Avian host community structure and prevalence of West Nile virus in Chicago, Illinois. Oecologia 159: 415-424.

8. Thomas L, Buckland ST, Rexstad EA, Laake JL, Strindberg S, et al. (2010) Distance software: design and analysis of distance sampling surveys for estimating population size. J Appl Ecol 47: 5-14.
Figure S1  Diagnostic plots for models explaining variation in *Culex* infection rate. Part A are the residuals for the model including the interaction of community force of infection and diversity (FOI*Div; see Table 1) and part B are the residuals for the model containing the individual force of infection for American robin, house sparrow, and European starling (see Table 2). Symbols in the residual plot indicate site and color indicates year.
Table S1. Host selection ratios for *Culex pipiens* collected in 11 field sites in southwest suburban Chicago, Illinois, 2005-2008. Includes avian species that were not observed in blood meals at a site (given a value of one) and those that were not recorded during avian surveys (given value of lowest observed bird density).

| Host                        | Site 1 | Site 3 | Site 5 | Site 7 | Site 10 | Site 11 | Site 12 | Site 15 | Site EC | Site SC | Site WW |
|-----------------------------|--------|--------|--------|--------|---------|---------|---------|---------|---------|---------|---------|
|                             | \(\hat{w}_1\) | \(\hat{w}_2\) | \(\hat{w}_3\) | \(\hat{w}_4\) | \(\hat{w}_5\) | \(\hat{w}_6\) | \(\hat{w}_7\) | \(\hat{w}_8\) | \(\hat{w}_9\) | \(\hat{w}_{10}\) | \(\hat{w}_{11}\) |
| American Crow               | 2.85   |        |        |        |         |         |         |         |         |         |         |
| American Goldfinch          | 2.30   | 4.84   | 1.32   | 3.37   | 0.91    | 0.84    | 1.84    | 1.20    | 0.92    |         |         |
| American Kestrel            | 282.16 |        |        |        |         |         |         |         |         |         |         |
| American Robin              | 0.94   | 1.07   | 1.96   | 2.00   | 0.97    | 10.13   | 1.25    | 1.12    | 0.32*   | 0.92    |         |
| Baltimore Oriole            |        | 42.11  |        | 34.94  | 43.54   |         |         |         |         |         | 52.85   |
| Black-capped Chickadee      | 5.98   |        |        | 49.18  | 4.43    | 3.59    | 14.00   |         |         |         |         |
| Brown-headed Cowbird        | 10.94  | 10.45  | 10.09  | 2.70   | 2.19    | 0.95    | 13.12   |         |         |         |         |
| Blue Jay                    | 10.23  | 5.37   | 4.89   | 18.87  | 4.99    | 2.73    | 3.99    | 12.27   |         |         |         |
| Brown Thrasher              |        |        |        |        | 65.56   |         |         |         |         |         |         |
| Cedar Waxwing               | 2.70   |        |        | 106.54 | 1.33    | 1.08    | 1.27    |         |         |         |         |
| Chipping Sparrow            | 3.24   | 10.20  | 9.28   | 2.24   | 1.93    | 0.96    | 1.94    | 0.54    |         |         |         |
| Common Grackle              | 2.27   | 0.95   | 0.29   | 0.84   | 0.67    | 0.51    | 0.08*   | 1.12    | 0.23    | 0.89    | 0.91    |
| Cooper's Hawk               | 198.39 |         |         |         |         |         |         |         |         |         |         |
| Common Yellowthroat         |        |        |        |        |         |         |         |         |         |         | 2.60    |
| Downy Woodpecker            | 15.72  |        |        | 5.61   |         |         |         |         |         | 6.65    | 6.81    |
| Eastern Kingbird            | 11.36  |        |        |        |         |         |         |         |         |         |         |
| European Starling           | 3.88   | 0.51   | 3.24   | 0.48   | 0.38    | 0.43    | 0.12*   | 0.79    | 0.25    | 1.12    |         |
| Gray Catbird                | 6.62   |        |        | 2.63   | 6.34    | 6.82    | 2.07    | 0.57    |         |         |         |
| Hairy Woodpecker            |        |        |        |        |         |         |         |         |         |         | 0.10*   |
| House Finch                 | 2.29   | 4.81   | 4.38   | 33.81  | 3.35    | 25.42   | 6.71    | 2.01    | 14.30   | 32.95   |         |
| House Sparrow               | 0.14*  | 0.51   | 0.38*  | 0.45   | 0.17*   | 0.29*   | 0.13*   | 0.07*   | 1.77    | 0.78    | 0.30    |
| House Wren                  | 9.77   | 10.26  | 18.67  |        | 5.16    | 49.18   | 3.86    | 19.62   | 7.62    |         |         |
| Indigo Bunting              | 37.42  |        |        |        |         |         |         |         |         | 12.28   | 56.58   |
| Killdeer                    |         |        |        |        |         |         |         |         |         | 0.96    | 4.20    |
| Mallard                     |         |        |        |        |         |         |         |         |         |         | 0.61    |
| Mourning Dove               | 1.70   | 1.54   | 1.15   | 0.34   | 0.54    | 2.10    | 0.38    | 0.40    | 2.61    | 3.44    | 2.64    |
| Monk Parakeet               |         |        |        |        | 0.03*   |         |         |         | 28.03   |         |         |
| Northern Cardinal           | 1.93   | 12.18  | 9.98   | 6.42   | 1.42    | 4.60    | 1.42    | 8.92    | 2.35    | 2.26    | 3.71    |
| Red-eyed Vireo              | 28.16  |         |        |         |         |         |         | 9.82    |         |         | 32.17   |
| Ring-necked Pheasant        |         |        |        |        |         |         |         |         |         |         | 45.80   |
| Rock Pigeon                 | 0.32   |        |        | 0.89   |         |         |         |         |         |         |         |
| Red-winged Blackbird        | 0.46   |        |        | 0.26   | 0.18*   | 0.18*   |         |         |         |         |         |
| Scarlet Tanager             |         |        |        | 49.18  |         |         |         |         |         |         |         |
| Song Sparrow                | 141.08 |         |        | 4.51   | 16.85   | 0.84    | 0.63    | 1.57    |         |         |         |
| Swamp Sparrow               | 134.34 |        |        | 106.54 |         |         |         |         |         |         |         |
| Veery                       |         |        |        |        |         |         |         |         |         |         | 2.07    |
| Warbling Vireo              |         |        |        |        |         |         |         |         |         |         | 13.65   |
| Willow Flycatcher           |         |        |        |        |         |         |         |         |         |         | 67.21   |
| Northern Flicker            |         |        |        |        |         |         |         |         |         |         | 9.52    |
| Yellow Warbler              |         |        |        |        |         |         |         |         |         |         | 49.18   |

*Sample size 18 27 31 29 23 43 158 21 35 19 23

*Scientific names can be found by accessing the American Ornithologists' Union Check-list (http://www.aou.org/checklist/north/index.php).

*Italicized host selection ratios imply that a blood meal of one or a relative density of the lowest observed bird was assigned.

*Statistically significant non-random host selection at \(P < 0.05\).
Table S2. Number of infectious *Cx. pipiens* (i.e. force of infection) resulting from feeding on different avian hosts by site, suburban Chicago, Illinois, 2005-2008. Number of infectious mosquitoes were calculated by $B_i^2 \cdot C_i$, where $B$ is the proportion of blood meals from host species $i$ and $C$ is the host competence index. All sites combined includes additional sites with sample sizes of < 20 *Cx. pipiens* blood meals. Species are ranked based on force of infection values from highest to lowest for all sites combined.

| Host species | $C_i$ | 1  | 3  | 5  | 7  | 10 | 11 | 12 | 15 | EC | SC | WW | All sites |
|--------------|------|----|----|----|----|----|----|----|----|----|----|----|---------|
| American Robin | 1.04 | 0.084 | 0.019 | 0.030 | 0.036 | 0.332 | 0.037 | 0.573 | 0.132 | 0.507 | 0.045 | 0.051 | 0.160 |
| House Sparrow | 1.23 | 0.011 | 0.109 | 0.073 | 0.081 | 0.005 | 0.028 | 0.004 | 0.002 | 0.001 | 0.002 | 0.009 | 0.017 |
| House Finch | 1.28 | 0.003 | 0.004 | 0.001 | 0.011 | 0.006 | 0.022 | 0.001 | 0.007 | 0.000 | 0.009 | 0.009 | 0.004 |
| Northern Cardinal | 0.38 | 0.001 | 0.000 | 0.018 | 0.002 | 0.000 | 0.002 | 0.000 | 0.024 | 0.000 | 0.000 | 0.005 | 0.002 |
| Blue Jay | 2.38 | 0.000 | 0.000 | 0.000 | 0.012 | 0.000 | 0.000 | 0.001 | 0.000 | 0.000 | 0.000 | 0.000 | 0.007 |
| Mourning Dove | 0.09 | 0.005 | 0.001 | 0.000 | 0.000 | 0.000 | 0.005 | 0.000 | 0.000 | 0.001 | 0.004 | 0.000 | 0.001 |
| European Starling | 0.17 | 0.002 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.001 | 5.78E-05 | 1.64E-05 |
| American Kestrel | 0.78 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 1.65E-05 |
| House Wren | 0.77 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 1.64E-05 |
| Scarlet Tanager | 0.77 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 1.64E-05 |
| Cedar Waxwing | 0.77 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 1.64E-05 |
| Common Grackle | 1.40 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 1.32E-05 |
| Chipping Sparrow | 0.97 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 9.14E-06 |
| Song Sparrow | 0.97 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 9.14E-06 |
| Black-capped Chickadee | 0.77 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 7.27E-06 |
| Red-winged Blackbird | 0.42 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 4.00E-06 |
| Common Canary | 1.28 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 3.01E-06 |
| American Goldfinch | 1.28 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 3.01E-06 |
| Cooper's Hawk | 0.78 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 1.84E-06 |
| Swainson's Thrush | 0.12 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 1.11E-06 |
| Veery | 0.39 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 9.08E-07 |
| Gray Catbird | 0.08 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 7.34E-07 |
| Brown Thrasher | 0.19 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 4.38E-07 |
| Northern Flicker | 0.14 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 3.35E-07 |
| Rock Pigeon | 0.00 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.00E+00 |
| Sample size | 21 | 37 | 41 | 43 | 30 | 53 | 168 | 28 | 40 | 24 | 36 | 652 |

*Scientific names can be found by accessing the American Ornithologists' Union Check-list ([http://www.aou.org/checklist/north/index.php](http://www.aou.org/checklist/north/index.php)).