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RESEARCH ARTICLE

Radar analysis of fall bird migration stopover sites in the northeastern U.S.

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ABSTRACT

The national network of weather surveillance radars (WSR-88D) detects flying birds and is a useful remote-sensing tool for ornithological study. We used data collected during fall 2008 and 2009 by 16 WSR-88D radars in the northeastern U.S. to quantify the spatial distribution of landbirds during migratory stopover. We geo-referenced estimates based on radar reflectivity, of the density of migrants aloft at their abrupt evening exodus from daytime stopover sites, to the approximate locations from which they emerged. We classified bird stopover use by the magnitude and variation of radar reflectivity across nights; areas were considered "important" stopover sites for conservation if bird density was consistently high. We developed statistical models that predict potentially important stopover sites across the region, based on land cover, ground elevation, and geographic location. Large areas of regionally important stopover sites were located along the coastlines of Long Island Sound, throughout the Delmarva Peninsula, in areas surrounding Baltimore and Washington, along the western edge of the Adirondack Mountains, and within the Appalachian Mountains of southwestern Virginia and West Virginia. Locally important stopover sites generally were associated with deciduous forests embedded within landscapes dominated by developed or agricultural lands, or near the shores of major water bodies. Preserving or enhancing patches of natural habitat, particularly deciduous forests, in developed or agricultural landscapes and along major coastlines could be a priority for conservation plans addressing the stopover requirements of migratory landbirds in the northeastern U.S. Our maps of important stopover sites can be used to focus conservation efforts and can serve as a sampling frame for fieldwork to validate radar observations or for ecological studies of landbirds on migratory stopover.

Keywords: landbird migration, stopover distribution, WSR-88D radar, predictive mapping

Análisis por radar de los sitios de parada migratoria en otoño en el noreste de Estados Unidos

RESUMEN

La red nacional de radares de vigilancia del clima (WSR-88D) detecta aves volando y es una herramienta útil de monitoreo remoto para estudios ornitológicos. Usamos datos recolectados en otoño de 2008 y 2009 por 16 radares WSR-88D en el noreste de los Estados Unidos para cuantificar la distribución espacial de aves terrestres durante sus paradas migratorias. Referenciamos geográficamente los estimados de la densidad de aves migrantes en vuelo durante sus eventos abruptos de éxodo nocturno desde los sitios de parada diurnos basándonos en la reflectividad del radar, que nos permitió establecer la localización aproximada desde donde emergieron. Clasificamos el uso de sitios de parada migratoria por la magnitud y variación de la reflectividad del radar a través de diferentes noches; si la densidad de aves era consistentemente alta en determinadas áreas, éstas fueron consideradas como sitios de parada 'importantes' para su conservación. Desarrollamos modelos estadísticos que predicen sitios de parada potencialmente importantes a través de la región con base en información sobre cobertura del terreno, elevación y localización geográfica. Se localizaron grandes áreas de sitios de parada regionalmente importantes a lo largo de la costa de la bahía de Long Island, la península de Delmarva, áreas alrededor de Baltimore y Washington, el borde occidental de las montañas Adirondack y en las montañas Apalaches del suroccidente de Virginia y Virginia Occidental. Los sitios de parada localmente importantes generalmente estuvieron asociados con bosques caducifolios embebidos en paisajes dominados por tierras agrícolas o transformadas, o cerca de las costas de importantes cuerpos de agua. La preservación o el mejoramiento de parches de hábitat natural, particularmente de bosques caducifolios en los paisajes agrícolas o transformados y a lo largo de las principales costas, deberían ser una prioridad en los planes de conservación dirigidos hacia los requerimientos de los sitios de parada migratoria de aves terrestres en el noreste de Estados Unidos. Nuestros mapas de sitios importantes de parada migratoria pueden ser usados para enfocar los esfuerzos de conservación, y pueden servir como marco de referencia para hacer trabajo de campo que valide las observaciones hechas con radar o para estudios ecológicos de aves terrestres en los sitios de parada migratoria.

Palabras clave: distribución de sitios de parada migratoria, mapeo predictivo, migración de aves terrestres, radar WSR-88D

INTRODUCTION

Identification and protection of important migration stopover areas is fundamental to the development of comprehensive strategies to conserve migratory bird populations (Moore and Simons 1992, Hutto 2000, Rich et al. 2004, Mehlman et al. 2005, Moore et al. 2005, Faaborg et al. 2010a, 2010b), many of which have declined significantly over recent decades (Robbins et al. 1989, Askins et al. 1990, Sauer et al. 2011). Losses in the extent and quality of habitats are the primary causes of population declines during the breeding and wintering periods of the annual cycle (Faaborg et al. 1995, 2010b, Sherry and Holmes 1995), and conservation efforts for migratory landbirds in North America have focused on protecting or enhancing breeding habitat. However, migration may be the period in the annual cycle when mortality is highest (Sillett and Holmes 2002, Newton 2006), and therefore it likely has an important role in limiting migratory bird populations (Sherry and Holmes 1995, Hutto 2000, Newton 2006).

Most migratory landbirds migrate at night, embarking en masse at around dusk and landing sometime before dawn. They take up to one third of each annual cycle to complete their biannual migrations, spending upward of 95% of this time resting and refueling rather than in actual migratory flight (Hedenström and Alerstam 1997, Alerstam 2003). Their successful migration thus depends on the availability of suitable stopover sites. Although landbirds collectively migrate along a broad front, with a seemingly large number of places to stop en route, in parts of North America a shortage of favorable habitats may threaten successful or timely migration (e.g., Tankersley and Orvis 2003). This is of particular concern for the northeastern U.S., where human-dominated land-use/cover currently occupies 78% of the land area and is increasing faster than in other regions (Brown et al. 2005).

The national network of weather surveillance radars (model WSR-88D) routinely detects a variety of bird movements across the U.S. In particular, these radars have been used to observe the spatial distribution of landbirds during migratory stopover by taking an instantaneous measure of the electromagnetic radiation reflected from birds in the radar beam as they begin to leave stopover sites at the abrupt onset of nocturnal migratory flight (e.g., Gauthreaux and Belser 2003, Diehl and Larkin 2005, Bonter et al. 2009, Buler and Diehl 2009, Buler and Moore 2011). Radar ''reflectivity'' is positively correlated to the density of birds aloft, and provides an estimate of relative bird density across the area sampled (Gauthreaux and Belser 1998, 1999, Diehl et al. 2003). By observing the magnitude and variability of bird density through one or more migration seasons, the radars allow for a spatially explicit assessment of the relative use of migratory stopover sites across large geographic areas.

We used data collected by WSR-88D radars to map landbird use of stopover sites during the fall migration across the northeastern U.S. We quantified relative bird densities across two migration seasons within roughly 80 km of the radars (i.e. radar-sampled areas) to identify ''important'' stopover sites that receive high and consistent use by landbird migrants, and developed statistical models to predict potentially important stopover sites across the study region, using environmental characteristics that explain variability in relative bird density within the radar-sampled areas.

Characterizing migrant stopover use of sites by the magnitude and variance in bird density can help identify important stopover areas so that scarce conservation resources can be invested most efficiently (Mehlman et al. 2005). However, from an ecological perspective, the actual intrinsic quality or function of a site for refueling and/or resting is not directly measured by characterizing stopover use rates. Along the Gulf of Mexico coast, sites from which migrants consistently leave in high density include both food-rich bottomland hardwood forests, where migrants stop over for several days, and potentially food-poor sites that may only offer a safe place to land (Buler and Moore 2011). Areas with high seasonal mean bird density but large variance are used relatively infrequently at high density, likely only as refuge during poor weather conditions that are highly stochastic in space and time and difficult to predict. Thus, sites that are consistently used in relatively high densities may be the best targets for conservation due to their high intrinsic (e.g., relatively abundant food resources) and/or extrinsic (e.g., proximity to a geographical barrier) value. The aim is to focus conservation on stopover sites that support the most birds per unit area regardless of the reason that birds may use them. The stopover use maps we produced can be used as decision support tools for conservation planning, or as a sampling frame for field surveys to ''ground truth'' the radar and analytical results or for targeting ecological studies of landbirds during migratory stopover to identify the ecological function of important sites.

METHODS

WSR-88D Data and Operation

We analyzed data collected by 16 WSR-88D radars in the northeastern U.S. (Figure 1). These radars, operated by the National Weather Service within the National Oceanic and Atmospheric Administration (NOAA) or the Department of Defense (DOD), transmit horizontally polarized electromagnetic radiation at a wavelength around 10 cm (S band) and a nominal peak power of 750 kW with a half-power beam width (3 dB) of 0.95° (Crum and Alberty 1993). The radars measure the strength of the returned radiation from airborne "targets" (e.g., birds) within a sampled volume of airspace in units of Z (reflectivity) on a logarithmic scale to the nearest half decibel (0.5 dB), as well as the mean speed (in knots) and direction of movement of targets relative to the radar (radial velocity). WSR-88D data are archived by NOAA's National Climatic Data Center (NCDC) and are freely available for download.

The radars make a "volume scan" of the airspace every 6 or 10 min, depending on whether they are set to operate in "precipitation" or "clear air" mode. Each volume scan is composed of a set of 5–14 360° "sweeps" of the antenna from its fixed location at tilt angles ranging from 0.5° to 19.5° above the horizon. For each tilt-angle sweep, data are measured within "sample volumes" from 2 to 230 km in range from the radar along each of 720 radials. We used Level II data for analysis, which have sample volume dimensions of 250 m in range by 0.5° in diameter (i.e. "super" resolution). However, data from the KDOX and KTYX radars, operated by the DOD, are archived at the coarser "legacy" sample volume resolution of 1 km x 1°.

Data screening and selection. We obtained radar data collected during the periods of peak fall landbird migration (15 August to 7 November) in 2008 and 2009 from the NCDC archive. We visually screened radar sweeps from the lowest tilt angle to identify days when precipitation was present at dusk or there was extreme refraction of the radar beam toward the ground (aka anomalous propagation), which can occur under certain atmospheric conditions, and excluded these days from further analysis. For remaining days, we assessed the air speed of radar targets, using radar radial velocity data collected ~3 hr after dusk (typically the peak of nocturnal migration), to determine whether targets were dominated by migrating birds or insects. For those WSR-88D stations where weather balloons are launched ($n = 10$), we obtained upper-air sounding data (wind speed and direction) archived by the University of Wyoming (http://weather.uwyo.edu/upperair/sounding.html). We estimated mean target groundspeed and direction from radial velocity data from the 3.5° tilt-angle radar sweep, using methods outlined by Browning and Wexler (1968) at heights where wind speed and direction were sampled. We then subtracted the vectors for wind speed and direction from the vectors of target groundspeed and direction to derive mean target airspeed. We considered radar sweeps with mean target airspeed >5 m s^{-1} to be dominated by birds (Larkin 1991, Gauthreaux and Belser 1998). For WSR-88D stations without atmospheric sounding data, we obtained surface wind data from the nearest weather station in the NCDC archive. We then visually screened the radial velocity data from the 0.5° tilt-angle radar sweep, and considered the data to be dominated by birds if a majority of sample volumes had radial velocities >5 m s^{-1} faster than the surface wind speed. We dropped from further analysis nights dominated by slow-flying targets. However, radar reflectivity of nights we retained could contain some bats (Fleming and Eby 2003) and insects, particularly on warm nights in early autumn when insects are still active (Alerstam et al. 2011).

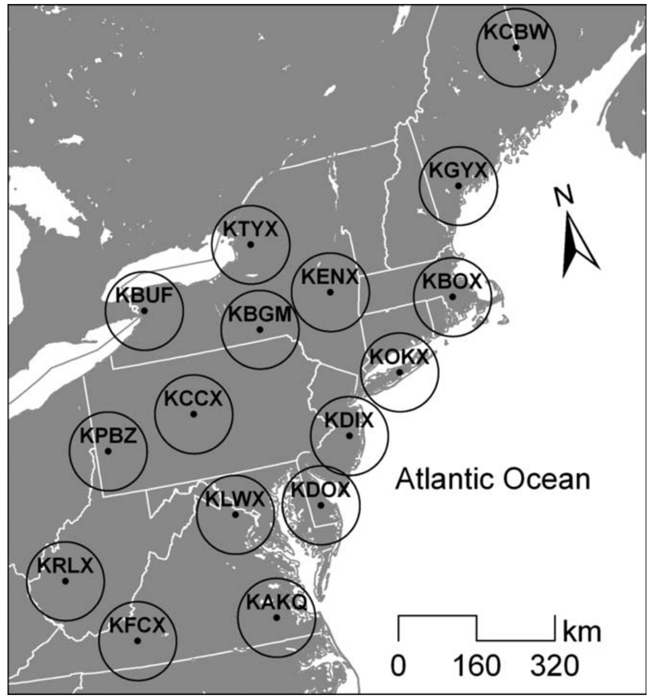

FIGURE 1. Locations and call signs of 16 WSR-88D radars and their 80-km–radius sampling areas (circles).

Radar Base Grid and Data Masking Maps

We produced base grid maps for each WSR-88D station for geo-referencing the radar data and extracting landscape characteristics for analyses. Each base grid is a polar grid of 285,120 polygons with spatial resolution of 0.5° × 250 m around the radar out to a distance of 100 km, with each polygon corresponding to the 2-dimensional boundary of a radar sample volume. Polygons of KDOX and KTYX base grids had a spatial resolution of 0.25° × 1 km following spatial realignment of original 1° sample volumes to the nearest 0.25° to mitigate the small mechanical variability in horizontal azimuth sampling (Buler and Diehl 2009). The coarser resolution of these two radars (142,650 polygons) limits only the finest-scale associations of radar measures to ground features and does not affect broader-scale patterns in bird stopover densities.

Topography and human infrastructure (e.g., tall buildings) can partially or completely block the radar beam, limiting the area sampled around some radars. We used the base grids to aid in defining the area sampled by each radar. Data from individual sample volumes were masked (i.e. excluded from data analyses) if (1) there was partial or complete blockage of the 0.5° tilt-angle radar beam due to topography or human infrastructure, (2) they were located over open water, or (3) persistent ground clutter contaminated their reflectivity measures (Figure 2). We also excluded data from all sample volumes $\leq$7.5 km from each radar due to unpredictable intermittent ground clutter echoes near the radar antenna. We used the base grids to determine the mean ground elevation (to the nearest 10 m) beneath sample volumes, using elevation data from the National Elevation Dataset (resolution 1 arc-second) assembled by the U.S. Geological Survey. We then calculated the amount of beam blockage due to topography, using the simplified beam interception function described by Bech et al. (2003) assuming standard atmospheric conditions. Radar data from sample volumes with $\geq$25% of radar beam blockage were not included in analyses. Finally, we identified, and excluded from analyses, sample volumes with persistent ground clutter contamination or partial radar beam blockage from human infrastructure by determining the frequency of reflectivity detections for each sample volume across $\sim$4,000 daytime volume scans collected during June 2009, when birds were not migrating through the study region, following methods outlined in Buler et al. (2012b).

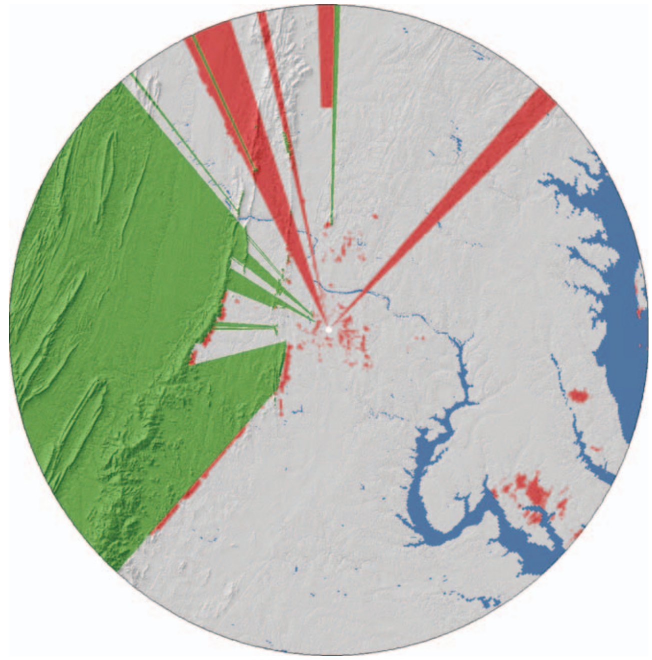

FIGURE 2. Masking map of the KLWX radar in Sterling, VA, showing sample volumes excluded from analyses due to (1) topographic beam blockage (green), (2) dominance of open water (blue), or (3) persistent ground clutter contamination and other sources of beam blockage (red).

Data Preprocessing

For suitable days dominated by bird targets, we interpolated reflectivity measures of individual sample volumes to when the sun reached an elevation angle of 5.5° below horizon ($\sim$30 min after sunset), using inverse distance weighting of the time differences between the radar volume scans collected immediately before and after the target sun elevation time point, following Buler et al. (2012a). This sun elevation corresponded with the typical initial appearance of birds within at least 50 km range from the radar and before they became spatially dispersed from their ground sources. The purpose of the interpolation is to reduce (1) temporal sampling error among nights due to the relatively coarse sampling rate of WSR-88D, and (2) sampling bias within a radar sweep due to the systematic change in sun elevation along an east–west gradient. The interpolation produces an instantaneous measure of the abrupt exodus of birds at the onset of migratory flight that is standardized in time across the radar-sampled area and across days.

The radar beam spreads as it travels away from the radar antenna and differentially samples the vertical distribution of birds in the airspace. This creates bias in reflectivity measures and precludes the direct comparison of raw radar measures at different ranges and at different ground elevations. To correct for these measurement biases, we adjusted the interpolated radar data using the algorithm of Buler and Diehl (2009) with several refinements.

The algorithm characterizes the vertical distribution of birds by determining the mean apparent vertical profile of reflectivity (VPR). When computing VPRs, we improved the weighting of reflectivity measures within the radar beam by using a Gaussian distribution of the power in the beam rather than a uniform power distribution. Additionally, because 25% of radar beam power is outside the 3-dB beam width, we modeled beam characteristics using a 6-dB beam width, which incorporates 94% of the radar power. We also incorporated the variability in mean ground elevation across ranges into beam height calculations and filtered out data from partially blocked beams. We identified the effective maximum height of birds in the airspace as the maximum beam height of the 0.5° tilt-angle beam at the range from the radar where the ratio of the mean reflectivity of the 1.5° beam to the mean reflectivity of the 0.5° beam is $\leq$0.005. This denotes the range at which the 1.5° beam begins to pass completely above the distribution of birds in the airspace. We then set any reflectivity values at heights above the effective maximum bird height to zero. This improvement helped remove contamination in the VPR from occasional high altitude non-bird targets (e.g., fog or dust).

Radars never detected birds emanating from water away from shorelines in the data we analyzed. However, sometimes exodus of birds from land areas extends into sample volumes over water adjacent to the borders of water bodies. Because the airspace over water seldom contained birds at exodus, we excluded radar data for computing VPRs from those sample volumes with $\geq$75% of their associated base grid polygon composed of water. We determined the amount of open water beneath sample volumes using data from the National Land Cover Dataset (NLCD 2006; Fry et al. 2011). We included sample nights when there was precipitation or sea clutter detected over water for coastal radars since water was not an area of interest. Consequently, in our figures of radar data there are some areas of strong reflectivity over water that were not due to birds, specifically around the KOKX radar.

We processed radar data using Program BIRDS (Bias Improvement of Radar Data System), developed at the University of Delaware to process WSR-88D data for quantifying migrant bird distributions on the ground. The software, available on request from the first author, is a system of Java scripts, Python scripts, and Fortran 95 code that runs within a UNIX environment. BIRDS converts batched radar reflectivity data (i.e. data from multiple nights at one radar station) to ASCII format, performs the spatio–temporal data interpolation with respect to a specified sun angle, estimates the VPR and partial beam blockage due to topography, adjusts reflectivity measures for measurement bias, and provides summary statistics of adjusted reflectivity for every sample volume across sampling days.

Data Analysis

As the radar beam travels up and away from the radar antenna, it increasingly samples less of the altitudinal distribution of birds in the airspace, reaching a point at which it passes completely over birds aloft. Accordingly, for each day dominated by bird targets we censored sample volumes that observed $\leq$10% of the VPR or had a bias-adjustment factor <0.05 (i.e. adjusted reflectivity is >20 times raw reflectivity), considering them as "non-detects." The detection limits of censored values for individual sample volumes varied among days due to the interaction of 3 main factors. First, atmospheric conditions influence how the beam propagates through the air, producing variability among days in the sampling heights of the radar beam for a given sample volume. Second, the exact timing of when birds initiate nocturnal migratory flight, and their vertical distribution in the airspace at the time they are sampled, varies among days, creating variability in VPRs. Third, the numbers of birds engaging in migratory flight affects the extent of attenuation of the radar beam's power as the beam passes through target-dense airspace, creating variability among days in the sensitivity of the radar for detecting birds. Thus, our radar datasets contain variable detection limits and are multiply censored.

The semiparametric robust linear regression on order statistics (ROS) method has been evaluated as one of the most reliable procedures for estimating summary statistics of multiply censored data (Lee and Helsel 2005). The observed uncensored values are combined with modeled censored values (non-detects) to estimate summary statistics of the entire population. ROS is applicable to any dataset that has 0 to 80% of its values censored. However, we conservatively restricted analysis to sample volumes that had <25% of their values censored. We used the R software (R Development Core Team 2011) package NADA (Lee and Helsel 2005) to perform the ROS analyses. For each sampling day, we used the minimum observed reflectivity value among sample volumes at a given range to determine the range-specific censoring limit values for the ROS algorithm. We summarized bias-adjusted reflectivity (hereafter "reflectivity") measures using ROS for each sample volume by pooling radar data across days and years. For each sample volume we estimated the geometric mean reflectivity (MN) as a relative measure of the mean daily stopover density of birds and the coefficient of variation of reflectivity (CV) as a measure of the daily variability in bird stopover density.

We used MN and CV to characterize radar-observed bird use of stopover sites by the magnitude and variation of reflectivity among sample volumes. Stopover use was first categorized into low (MN <50th percentile), medium (MN $\geq$50th percentile and <85th percentile), and high (MN $\geq$85th percentile) seasonal mean density. We further categorized high mean density as being (1) stable (CV $\leq$25th percentile), (2) of moderate variability (CV >25th percentile and <75th percentile), or (3) highly variable (CV $\geq$75th percentile) throughout the season. Stopover classifications of observed data are relative since percentile rankings were computed on a radar-by-radar basis (local context) or pooled across radars (regional context).

Modeling Bird Distributions

We used 5 variables that characterize landscape composition and location for building statistical models to predict MN and CV in portions of the study region not observed by the radars. These included the percent cover by hardwood forest, agricultural land, and human development; mean distance to the nearest major water body (e.g., Great Lakes, Atlantic Ocean); and mean ground elevation.

We first created a sampling grid of the entire study region composed of 637,626 1-km^2 polygons. For each grid polygon that contained radar-observed data ($n = 179{,}348$; 28% of all grid polygons), we computed the area-weighted average observed MN and CV from the portions of all radar sample volumes that fell within the boundary of the polygon.

We quantified the mean percent of land cover within 5 km of each grid polygon, following Buler et al. (2007), who found that density of migrating forest birds during stopover was most strongly correlated to forest cover measured within a 5-km–radius landscape. We used NLCD 2006 data, considering land cover types (NLCD value) Deciduous Forest (41), Mixed Forest (43), and Woody Wetlands (90) as hardwood forest, Pasture/Hay (81) and Cultivated Crops (82) as agricultural land, and all Developed classes (21–24) as human development. We first created a raster (25-m resolution) of the percent of each land cover type within a 5-km radius for all raster cells, and then calculated the mean land cover percentages across all raster cells within each grid polygon.

We applied multi-model inference within an information–theoretic approach to estimate the ability of predictor variables to explain variation in MN and CV using ordinary least-squares (OLS) linear regression (Burnham and Anderson 2002). Data for variables were log-transformed when necessary to help meet assumptions of normality for fitting models. We included latitude and longitude as additional predictor variables for OLS models to assess regional spatial patterns in reflectivity. We fit models using observed radar data from 25 unique subsets of grid polygons that were separated by $\geq$5 km to ensure spatial independence among landscape composition and reflectivity measures. Modeling results were nearly identical among the data subsets so we present the results from one example subset composed of 7,158 1-km^2 polygons. Predictor variables for this subset did not exhibit strong multicollinearity. Distance to the coastline and elevation had the strongest correlation at 0.734, followed by latitude and longitude at 0.671. We tested all 128 possible combinations of regression models excluding interaction terms. We used Akaike's Information Criterion (Akaike 1973) to rank models based on their ability to explain the data, and Akaike weights to estimate the relative likelihood of each model given the data. To determine the direction and magnitude of effect sizes for variables, we calculated the mean standardized regression coefficient across all models containing the variable of interest, and estimated precision using an unconditional variance estimator that incorporates model selection uncertainty (Burnham and Anderson 2002:162).

Because relationships of landbirds with their environment can vary over space during migratory stopover, even within the area observed by a single radar (e.g., Buler and Moore 2011), we built predictive models using geographically weighted regression (GWR). As the name implies, GWR implements a geographical weighting scheme that produces localized regression coefficients for individual locations (Fotheringham et al. 2002). By incorporating spatial variability in regression coefficients, GWR can better explain organism–environment relationships than OLS regression, which applies static global regression coefficients (Kupfer and Farris 2007, Miller and Hanham 2011). We used the GWR tool within ArcMAP 9.3.1 (Esri, Redlands, CA, USA) to perform the analyses. We used an adaptive spatial extent (the Gaussian kernel) of 100 nearest neighbors ($\sim$25-km radius) for fitting each local regression among the same subset of grid polygons used to exemplify the global linear regression modeling. We predicted reflectivity measures to the entire 1-km^2 polygon sampling grid, except for 12,119 (2%) grid polygons where local multicollinearity among predictor variables prevented predictions from being calculated. We performed GWR on the subset of data from all radars and on 16 additional data subsets in which we excluded data from one radar in turn among each subset. We then averaged predicted reflectivity measures produced across all 17 datasets. This approach allowed us to reduce the influence of potential sampling bias from any one radar. We characterized bird stopover use from mean predicted reflectivity measures according to the thresholds used for radar-observed data. Note, however, that stopover classifications of predicted data are relative at a regional scale since percentile rankings were computed for the whole of the study region.

RESULTS

Among all WSR-88D radars and years, we sampled evening migratory flights from 14% of potential days (382 of 2,720); the percent of potential days used from individual radars ranged from 8% to 23%. Overall, the reasons for excluding days included the presence of precipitation (49%), anomalous propagation of the radar beam (23%), contamination from non-precipitation sources such as insects or clutter from sea breezes (17%), no or weak bird-flight activity (8%), or missing or problematic data in the archive (3%). See Supplemental Material Appendix A for a table of specific sample nights for all radars. After incorporating masking maps and detection thresholds, individual WSR-88D radars effectively observed bird stopover density for a mean of 12,711 km^2 (range 4,278 to 21,318 km^2) of land throughout fall migration. Collectively, they effectively sampled 203,386 km^2 (32%) of the land area within the study region.

We present maps combining the seasonal MN and CV of reflectivity, classified into five stopover use categories

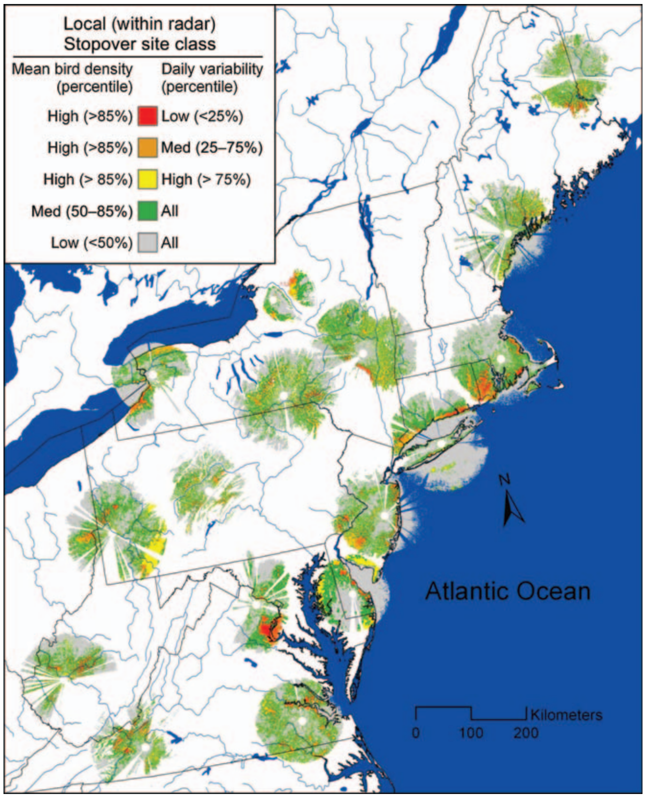

FIGURE 3. Map of locally classified (i.e. for each radar separately) radar-observed bird stopover density during fall 2008 and 2009 for 16 WSR-88D stations.

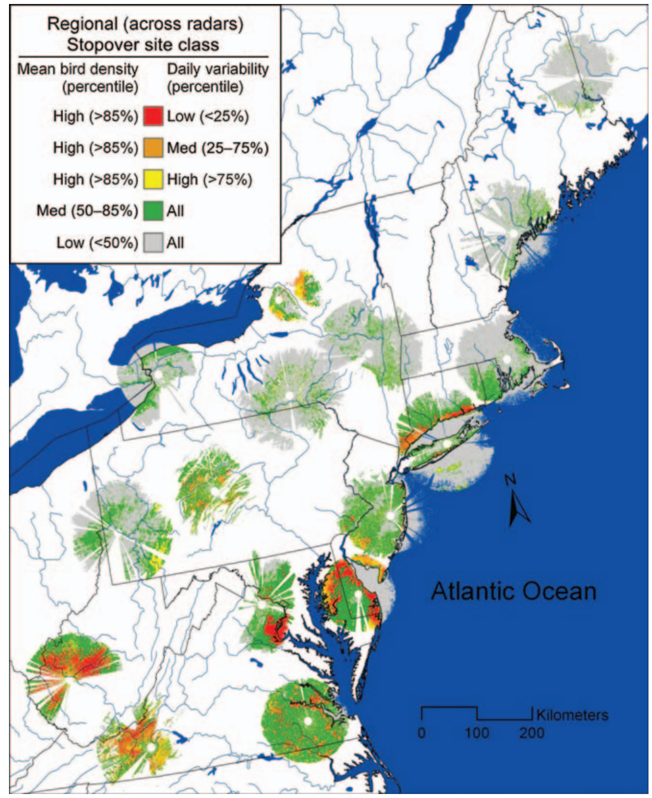

FIGURE 4. Map of regionally classified (i.e. data pooled across radars) radar-observed bird stopover density during fall 2008 and 2009 among 16 WSR-88D stations.

at two different spatial scales: local (Figure 3) and regional (Figure 4). The underlying data of the figures are identical. Qualitatively, classified reflectivity data from individual radars revealed that locally important stopover areas (i.e. consistently high bird stopover density; areas marked in red on Figure 3) coincide with hardwood forests embedded within landscapes dominated by developed and agricultural lands, as well as areas near the shores of major water bodies. For example, bird densities were particularly high within Rock Creek Park and other parks in the Washington, DC, metropolitan area (Figure 5), and Fairmount Park in Philadelphia had the highest bird densities within the area sampled by KDIX. Finer-scale maps of bird stopover patterns from individual radars can be found in Supplemental Material Appendix B, and GIS layers of individual radar maps are available upon request from the authors.

Large areas of regionally important stopover use, based on pooled observed data across radars, were located along the coastlines of Long Island Sound, throughout the Delmarva Peninsula, in areas surrounding Baltimore and Washington, along the western edge of the Adirondack Mountains, and within the Appalachian Mountains of southwestern Virginia and West Virginia (Figure 4). Differences in classifications between the two figures highlight differences between the local and regional context of migrant stopover use for particular locations. For example, forested habitats along the west coast of the Delaware Bay had high and consistent use both locally and regionally, whereas the locally classified high and consistent bird use areas along the eastern shore of Lake Erie had only moderate bird density in a regional context. Additionally, almost all areas around the KCBW radar in northeastern Maine had low to moderate migrant density in a regional context, but included all 5 use categories in a local context.

Quantitative analysis revealed that the full OLS model incorporating all predictor variables had the greatest weight of evidence among models and explained nearly half of the variability (unadjusted $R^2 = 0.44$) in MN (Table 1). Effect sizes of variables are important to consider since the large sample size (n >7,000) contributed to statistical significance for all variables considered. The strongest effects were associated with longitude, latitude, and distance from a major coastline (Table 2). MN increased to the south and west, and with proximity to the coast. Hardwood forest cover within a 5-km radius had a relatively moderate positive effect on MN. Elevation and

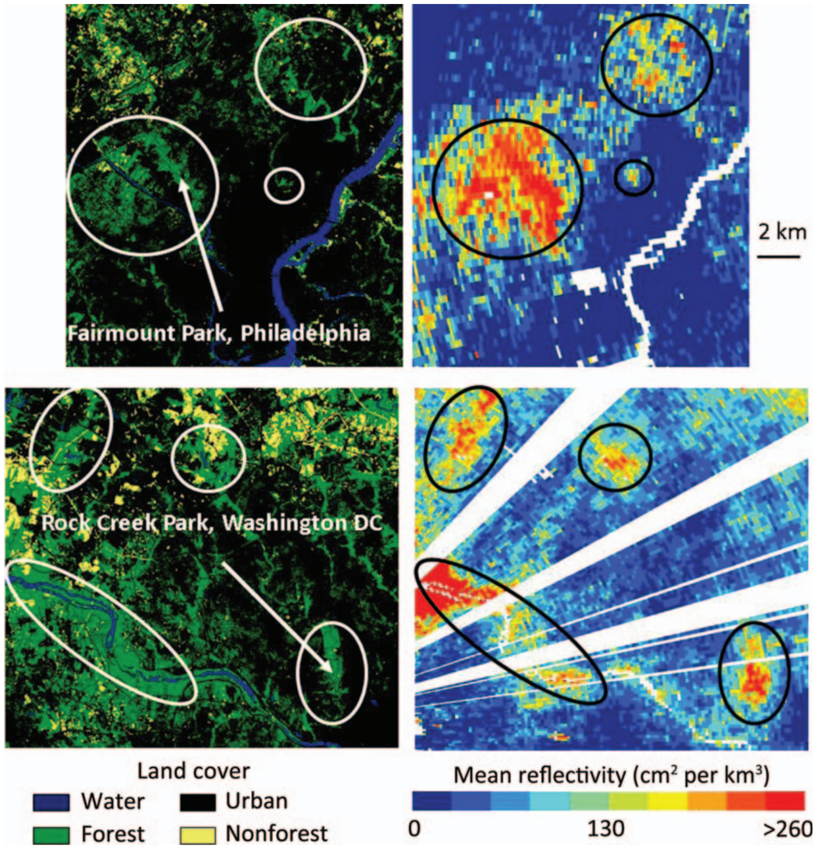

FIGURE 5. Examples (encircled) of urban forested areas that harbor high densities of migrating birds. Left panels depict land cover within portions of Philadelphia, PA (above) and Washington, DC (below). Right panels depict mean radar-observed bird stopover density during fall 2008 and 2009 within the same areas.

the amount of developed and agricultural lands within 5 km had weak negative effects on MN.

All predictor variables appeared in the top three OLS models that carried most of the weight of evidence, yet explained little of the variability (mean unadjusted $R^2 = 0.16$) in CV (Table 3). The relative effect sizes among individual predictors varied widely. Distance from a major coastline had the strongest effect size such that CV decreased with greater proximity to the coast. Longitude and latitude had moderate effects, with CV increasing to the north and east. With relatively weak effects, CV also increased with more human development and less hardwood forest cover within a 5-km radius. The effects of agricultural land and elevation on CV were negligible.

The predictive GWR models explained a considerable amount of the variability in MN (unadjusted $R^2 = 0.81$) and a moderate amount of the variability in CV (unadjusted $R^2 = 0.43$). The direction and magnitude of all predictor variable coefficients varied locally throughout the study region, and each predictor variable was locally uninformative (i.e. not significantly different from zero) for about half the region. MN tended to increase with greater

TABLE 1. Summary of top 5 ranked OLS models examining 7 predictor variables affecting the observed mean reflectivity (i.e. relative bird stopover density) during fall 2008 and 2009 among 16 WSR-88D radars within the northeastern U.S. See Methods for description of predictor variables. We tested 128 models using data from 7,158 1-km^2 polygons. We report the relative difference in AIC compared to the top-ranked model (Δ AIC), the AIC model weight (W), and the number of parameters in the model (K).

Model	Δ AIC	W	K	Rank
All predictors	0	0.767	8	1
All predictors except Agricultural land	2.9	0.201	7	2
All predictors except Agricultural land & Human development	7.6	0.018	6	3
All predictors except Human development	7.9	0.015	7	4
All predictors except Elevation	22.1	0.000	7	5

TABLE 2. Model-averaged standardized parameter estimates (± unconditional SE) of predictor variables in explaining the observed mean (MN) and coefficient of variation (CV) of reflectivity (i.e. relative bird stopover density) during fall 2008 and 2009 among 16 WSR-88D radars within the northeastern U.S. See Methods for description of predictor variables. Parameter estimates marked with (ns) have 95% confidence intervals that span zero and are considered not significant.

Variable	MN	CV
Longitude	−0.360 ± 0.017	0.189 ± 0.019
Latitude	−0.388 ± 0.017	0.238 ± 0.018
Elevation	−0.088 ± 0.018	−0.008 ± 0.022 (ns)
Distance from coastline	−0.373 ± 0.015	0.330 ± 0.016
Hardwood forest	0.187 ± 0.015	−0.063 ± 0.016
Agricultural land	−0.022 ± 0.011	−0.018 ± 0.013 (ns)
Human development	−0.034 ± 0.012	0.069 ± 0.014

amount of hardwood forest cover in the landscape. This is based on an evidence ratio equal to 5.1 of the number of significantly positive local coefficients to significantly negative local coefficients. MN also tended to increase with lower elevation (evidence ratio = 3.4), proximity to a major coastline (evidence ratio = 1.8), and lower amount of human development in the landscape (evidence ratio = 1.3). MN showed nearly equal directional response to the amount of agricultural land in the landscape (evidence ratio = 1.03). CV tended to increase with increasing distance from a major coastline (evidence ratio = 2.3), greater amount of human development in the landscape (evidence ratio = 1.6), and lower amounts of agricultural lands (evidence ratio = 1.5) and hardwood forest (evidence ratio = 1.3) in the landscape. CV showed nearly equal directional response to elevation (evidence ratio = 1.1).

The positive relationship between MN and forest cover was strongest where forest cover comprised 20–30% of the local region and decreased with increasing amount of local forest cover (Figure 6A). The relationship between MN and human development was negative only where human development comprised <10% of the local region (i.e. 53% of the sampled regions) and was positive for the remainder of local regions where human development comprised

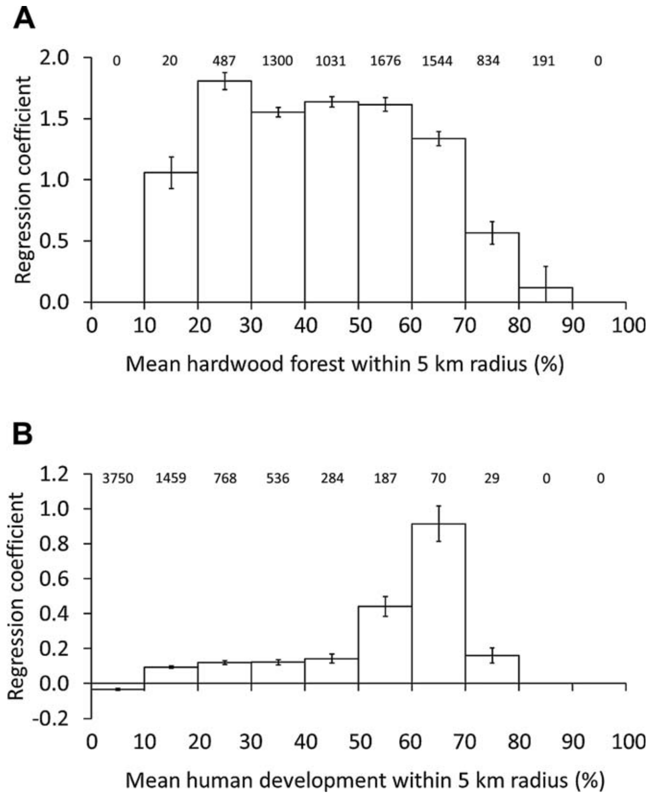

FIGURE 6. Mean ± SE local predictor variable coefficient values of (**A**) hardwood forest within a 5-km radius and (**B**) human development within a 5-km radius to explain mean reflectivity from GWR analysis of the example dataset (7,083 1-km^2 grid points). Coefficients are plotted by grouped intervals of 10% of the mean amount of the respective land cover type within a 5-km radius among the 100 nearest grid points used for each local regression. The number of regression coefficients included for each group is denoted above the bars.

>10% (Figure 6B). The magnitude of this positive relationship between human development and MN peaked when human development comprised 60–70% of the region, notably around Philadelphia and New York City. Regions with 50–60% human development cover that also exhibited a strong positive relationship primarily occurred around Boston, New York City, Philadelphia, and Washington, DC.

TABLE 3. Summary of top 5 ranked OLS models examining 7 predictor variables affecting the observed coefficient of variation of reflectivity (i.e. relative bird stopover density) during fall 2008 and 2009 among 16 WSR-88D radars within the northeastern U.S. See Methods for description of predictor variables. We tested 128 models using data from 7,158 1-km^2 polygons. We report the relative difference in AIC compared with the top-ranked model (Δ AIC), the AIC model weight (W), and the number of parameters in the model (K).

Model	Δ AIC	W	K	Rank
All predictors except Elevation & Agricultural land	0	0.365	6	1
All predictors except Elevation	0.1	0.351	7	2
All predictors except Agricultural land	1.8	0.146	7	3
All predictors	2.0	0.137	8	4
All predictors except Elevation & Agricultural land & Hardwood forest	14.8	0.000	5	5

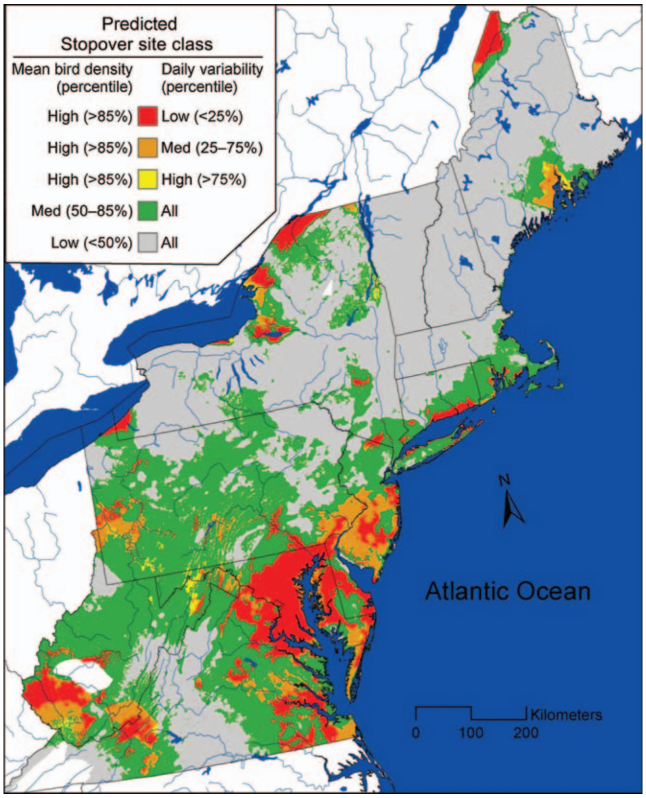

FIGURE 7. Map of regionally classified (i.e. data pooled across 16 WSR-88D sites) mean GWR-predicted bird stopover density during fall 2008 and 2009.

The classified map of predicted reflectivity highlights several areas that potentially are regionally important for migrating landbirds (Figure 7). These include areas within 50 km of the coastlines of Lake Erie, Lake Ontario, Long Island Sound, Chesapeake Bay, and Delaware Bay, and within 100 km of the Gulf of St. Lawrence, as well as forested landscapes within the Ohio Hills and Northern Cumberland Plateau physiographic areas in West Virginia, the Mid-Atlantic Ridge and Valley of Virginia, the Allegheny Plateau of Pennsylvania and New York, and the Northern Piedmont of Pennsylvania.

DISCUSSION

Migrating landbirds are known to stop over in almost any conceivable shelter, ranging from offshore oil platforms to urban parks to extensive forests. Weather surveillance radars provided us unprecedented comprehensive remotely sensed observations of migrants as they leave these stopover sites to embark on nocturnal flights at a rather fine grain (on the order of 10 ha) and across broad geographic extents to assess the relative use of stopover sites by migrating birds. During fall migration, we found that landbirds are ubiquitous throughout the northeastern U.S., being detected within essentially all radar sample volumes over land among all of the radars at some point during the migration season. However, not all stopover sites were used by migrants in equal densities or consistently throughout the migration season.

Our results emphasize that complex interactions among factors extrinsic and intrinsic to specific stopover sites influence migrant distributions across multiple spatial scales (Hutto 1985, Kelly et al. 1999, Moore et al. 2005, Buler et al. 2007, Buler and Moore 2011). At a broad geographic scale, migrants occurred at greater density along latitudinal and longitudinal gradients to the south and west, and near coastlines. At a finer scale, migrant densities were related to land-cover composition, but these relationships were not stationary in magnitude or direction and appeared to vary according to broader-scale landscape context.

In general, we found that the most consistent and highest bird stopover densities occurred primarily in (1) areas near the shores of major water bodies, (2) hardwood forest patches, particularly narrow floodplain forests of rivers and streams, embedded within landscapes dominated by developed and agricultural lands, and (3) hardwood forests within forest-dominated landscapes of the southwestern portion of the region (Ohio Hills and Northern Cumberland Plateau of West Virginia and Virginia). These patterns are consistent with other radar studies of landbird distribution patterns during migratory periods. Bonter et al. (2009) analyzed spring bird stopover within the Great Lakes basin and found that areas of high bird density were associated with near-shore areas and forest fragments in highly developed landscapes. Radar-observed bird stopover densities also were greater in near-coastal areas and hardwood forests along the Atlantic and Gulf coasts (Diehl et al. 2003, Gauthreaux and Belser 2003, Buler and Moore 2011). Extensive ground surveys provide additional evidence that migrant birds often concentrate along the Lake Ontario shoreline (Strobl 2010) and the Chesapeake Bay and Atlantic Ocean coasts of the Delmarva Peninsula (Watts and Mabey 1994). Strobl (2010) also found that abundance of migrants was greater in forest patches within agriculture-dominated landscapes than in forest patches in more forested landscapes.

Extrinsic physiographic features have an important influence on bird distributions during migratory stopover. We observed that migrant landbirds are consistently concentrated into near-shore areas of large water bodies, probably because coastal areas provide resting or landing places before or after overwater crossings (Diehl et al. 2003). Along the Atlantic Ocean, migrants appeared to concentrate more along coastlines oriented perpendicular to the generally southerly direction of migrant flight (e.g., Connecticut coast) than along more parallel-oriented coastlines (e.g., New Jersey coast, eastern coast of

Massachusetts). Additionally, we observed that migrants tended to concentrate to a greater extent on the down-migration side of some more inland coastlines (e.g., Delaware coast of Delaware Bay, south shore of James River and eastern Lake Erie) than on the up-migration side (e.g., New Jersey coast of Delaware Bay, north shore of James River and eastern Lake Erie).

The region-wide gradient of increased bird density to the south and west is another extrinsic factor that had a strong relationship with bird distributions. We propose two possible explanations for this pattern. First, the gradient may reflect a temporal sampling bias. However, we found no correlation between mean sampling day and latitude or longitude. More likely, the gradient of increased bird density reflects the ever-growing numbers of migrants that pass through the region to the southwest, the general migratory direction, through the course of the season. That is, fewer birds may migrate through and stop over in the more northeasterly parts of the region.

The consistently high bird densities associated with hardwood forests are likely due to a combination of intrinsic habitat qualities, including structural diversity of the vegetation, abundant food resources, and similarity to migrant breeding habitat. In general, tall and structurally diverse habitats support greater numbers of migratory bird species than habitats of low stature or simple structure (Petit 2000 and references therein, Rodewald and Matthews 2005). Bird stopover density also has been positively related to food abundance among and within habitats (e.g., Hutto 1985, Martin and Karr 1986, Rodewald and Brittingham 2004, Buler et al. 2007). Moreover, most of the landbirds migrating through the region are forest-nesting birds, and the habitats they select during migration may resemble the habitats used during the breeding season (Parnell 1969, Hutto 1985, Petit 2000, Rodewald and Brittingham 2004).

It is not surprising that intrinsic factors related to habitat composition had weaker effects than extrinsic factors in explaining bird stopover distributions across such a broad geographic area. Intrinsic factors generally operate at smaller spatial scales (Hutto 1985, Wiens 1989). Unfortunately, the resolution of the radar data is not fine enough to measure the airspace over pure land-cover types and resolve fine-scale patterns in habitat use. For example, only 3% of sample volumes over hardwood forests at KDIX are pure hardwood forest. Thus, there is noise in the data from sampling of mixed habitat types.

Radar observations demonstrated that forest patches in highly developed landscapes support some of the highest densities of migrating landbirds. This may be due to a "wicking effect" in which forest patches draw in migrants from the surrounding landscape, concentrating them, whereas in heavily forested landscapes the same number of migrants likely could be more evenly distributed and thus occur at lower densities. Additionally, the GWR results indicated the strongest positive relationships between bird density and forest cover occurred in areas with low amounts of forest cover in the landscape. Thus, there is likely greater motivation for forest migrants to concentrate into habitat patches. In their study of radar observations of bird stopover around the Great Lakes region, Bonter et al. (2009) suggest that birds likely concentrate in small forest fragments or the tree and shrub cover that exist in parks, gardens, and yards of residential areas, which may provide the most suitable stopover habitat in landscapes with little natural vegetation.

There may be an added effect of broad-scale attraction of migrants to cities that increases their densities in forest patches in developed landscapes. For half of the study region where human development was sparse (i.e. $<$10% of landscape), bird density was weakly negatively related to human development, suggesting that birds may avoid human development at a small scale in largely undeveloped landscapes. However, migrant density was positively related to human development in the other half of the region where human development was more prevalent and quite strongly around major cities. Bonter et al. (2009) found a similar positive relationship between bird density and the amount of human development in coastal areas of the Great Lakes, which they attributed to a confounding correlation between the amount of development and proximity to the coast. However, we controlled for proximity to the coast by using it as a covariate in the GWR models that produced the positive relationships of bird density with development. Thus, migrants appear to be attracted to developed landscapes at a broad scale. There is ample evidence that migrating birds are attracted to artificial light from human infrastructure at a local scale, but only scant evidence of attraction to the glow of city lights at a broad scale (Gauthreaux and Belser 2006). At the least, this intriguing possibility that migrants are drawn into urban areas by the intense glow of city lights warrants further investigation.

Our results support the idea that preserving existing patches of natural habitats, particularly forests, in developed and agricultural landscapes and in coastal areas could be a conservation priority to address the stopover requirements of migrant landbirds in the northeastern U.S. (Bonter et al. 2009). Mehlman et al. (2005) characterize these types of sites and other small habitat patches as "fire escapes" or "convenience stores," which offer shelter to migrants but lack sufficient food resources for them to fully replenish their energy reserves. They argue that conservation of fire-escape and convenience-store sites should take priority over more extensive food-rich "full-service hotel" sites because (1) they are otherwise unlikely to be identified and managed for conservation, (2) there are few remaining opportunities to protect them, and (3) they are at greater risk of being destroyed or degraded. Additionally, full-service hotel sites often are already under protection or targeted for conservation given their large extent or importance for other taxa.

Although we developed improvements in data quality control and reduction of radar measurement biases for this study, there remain challenges for the use of weather-radar data for analyzing bird stopover distributions. Major challenges include contamination of radar measures by non-bird targets, inability to identify targets to species, spatial displacement of birds from their true stopover locations, and coarse data resolution (Diehl and Larkin 2005, Ruth et al. 2008). Ongoing and future technological improvements will address some of these limitations (e.g., use of dual-polarized radars to discern birds from insects, Bachmann and Zrnić 2007). However, the combined effects of current limitations prevent adequate assessment of bird use of spatially restricted or rare habitats. For example, there are undoubtedly tidal wetlands that are critically important stopover areas for some bird species, and variability in bird density among different wetland areas. Weather radar is poor at discerning these patterns because birds emerging from narrow or small habitat patches (<10 ha) may be spatially displaced from them by the time they are sampled by the radar, and birds emerging from adjacent habitats contaminate the airspace over the small habitats, adding considerable noise to radar measures. Similarly, the scrub/shrub habitat type generally occurs in patches too small to explicitly assess its value as stopover habitat or to use this cover type for predictive modeling. Note also that an assessment of stopover use by particular bird species or species groups will require that the dates and locations examined be tailored to fit their natural history.

Areas with high topographic relief also pose challenges in using radar for mapping bird distributions. There is increased uncertainty in the accuracy of height distributions of birds above the ground, modeled beam propagation and blockage, and, consequently, adjusted radar measures in these areas. For example, there is the yet-untested possibility of localized variability in the height distributions of birds based on differences in the timing of migratory flight initiation or ascent rate depending on whether birds emerge from ridge or valley locations. Adjusted radar measures often indicate increased reflectivity within valleys that may in part be an artifact of the adjustment algorithm rather than truly greater bird density in low-lying areas in mountainous terrain. This is why we included elevation as a covariate in the regression models. Conversely, reflectivity measures can be inflated by radar energy reflected from the beam striking the ground at higher elevations.

We caution that our maps of classified migrant stopover density, while powerful tools for focusing conservation efforts, can oversimplify the dynamics of bird migration and the function of any particular area for stopover. Our classification scheme was coarse by having only a few categories to characterize seasonal patterns in bird use. The unclassified data include more precise measures of migrant stopover density at finer temporal scales and are available upon request to better elucidate dynamics of bird use. Additionally, the function of particular stopover areas may not be closely tied to the density of bird use and likely varies among migrants at a site within and among days. We reiterate that characterizing the flux of migrants from stopover sites provides only indirect evidence about the ecological value of sites. A better understanding of the function of sites for migratory birds must look beyond simple quantification of bird densities. We suggest that our bird stopover density maps should be complemented and integrated with studies of the intrinsic characteristics of specific sites or habitats (e.g., food resources, plant composition, vegetation structure) and the stopover behavior and ecology of birds using them (e.g., bird mass change, stopover duration, movement, mortality) to improve understanding of the quality or function of particular sites or habitats.

We view our predictive model as preliminary, and caution against relying too heavily on our region-wide predictive map (Figure 7) to assess the relative bird stopover use of sites outside of radar-sampled areas. The predicted bird densities within radar-sampled areas agreed quite well with radar-observed densities, but the accuracy of predicted bird densities elsewhere should be validated empirically.

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