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LETTER

Artificial light at night confounds broad-scale habitat use by migrating birds

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Abstract

With many of the world's migratory bird populations in alarming decline, broad-scale assessments of responses to migratory hazards may prove crucial to successful conservation efforts. Most birds migrate at night through increasingly light-polluted skies. Bright light sources can attract airborne migrants and lead to collisions with structures, but might also influence selection of migratory stopover habitat and thereby acquisition of food resources. We demonstrate, using multi-year weather radar measurements of nocturnal migrants across the northeastern U.S., that autumnal migrant stopover density increased at regional scales with proximity to the brightest areas, but decreased within a few kilometers of brightly-lit sources. This finding implies broad-scale attraction to artificial light while airborne, impeding selection for extensive forest habitat. Given that high-quality stopover habitat is critical to successful migration, and hindrances during migration can decrease fitness, artificial lights present a potentially heightened conservation concern for migratory bird populations.

Keywords

Artificial light at night, conservation, ecological modelling, generalized additive models, landbird migration, landscape ecology, machine learning, migratory stopover, stochastic boosting, weather surveillance radar.

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INTRODUCTION

At least 40% of the world's 10 000 bird species undertake annual migrations to exploit seasonal variation in resources (Newton 2008). Migratory bird populations have adapted morphological, physiological, and behavioral traits to mitigate hazards and negotiate what are often unpredictable conditions *en route* (Alerstam *et al.* 2003; Winkler *et al.* 2014). Migrating landbirds, for example, typically intersperse short sequences of nocturnal flight with extended stopover in terrestrial habitats, reflecting a critical trade-off between efficiency of acquiring energy reserves and the cost of carrying them (Alerstam 2011). At regional scales, migrating landbirds tend to move in broad fronts, and to concentrate in coastal areas either following wind-drift or to negotiate extended over-water crossings (Horton *et al.* 2016; LaFleur *et al.* 2016; Archibald *et al.* 2017). At finer spatial scales, these migrants select stopover habitat while descending to land as dawn approaches based on the availability and quality of food, using cues such as forest cover (Chernetsov 2006; Buler *et al.* 2007; Cohen *et al.* 2012). During stopover, scales of diurnal movement among nocturnal migrants are often less than 500 m (Chernetsov 2005; Cochran & Wikelski 2005; Cohen *et al.* 2012; Liu & Swanson 2015). However,

larger-scale nocturnal movements (tens to hundreds of kilometres) in non-migratory directions to re-locate to new stopover sites have also been reported (Mills *et al.* 2011; Brown & Taylor 2017).

Global declines among migratory bird populations have been linked to anthropogenic drivers such as land use and climate change (Robinson *et al.* 2009; Vickery *et al.* 2014). Citizen science data indicates that migrating landbirds in the U.S. use urbanized habitat more frequently during their journeys than on breeding or wintering grounds (Zuckerberg *et al.* 2016). Could artificial light at night partially account for this effect? Bright sources of artificial light are known to attract landbird migrants and (fledgling) seabirds in flight (Gauthreaux & Belser 2006; Poot *et al.* 2008; Rodríguez *et al.* 2015), and can increase mortality via collisions with anthropogenic structures (Longcore *et al.* 2013). However, artificial light could potentially also displace airborne migrants at broader scales. For example, within the northeastern U.S., migrating birds aloft are likely exposed consistently to the skyglow of large metropolitan areas, which can be perceived up to 300 km away (Olsen *et al.* 2014). Little is known about how migrating birds adjust their in-flight orientation, but cues based on both celestial light and the Earth's magnetic field are most likely involved (Chernetsov 2017), and the avian

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magnetic sense can be confounded by polarized light (Muheim *et al.* 2016).

Anthropogenic light levels have increased vastly over the past century, reaching ‘polluted’ levels – rendering the Milky Way indiscernible to the human eye – across at least 70% of the U.S. and 40% globally (Duffy *et al.* 2015; Falchi *et al.* 2016). It is however unknown whether a persistent influence of artificial light on migrants could actually pose a conservation concern, e.g. through a combination of light-associated mortality, deteriorated condition or disruptions to life histories (e.g. Legagneux *et al.* 2012), which together with carry-over effects could impact population dynamics (Harrison *et al.* 2011; Rushing *et al.* 2016). Alternatively, migrants could potentially mitigate such effects through behavioural plasticity (Winkler *et al.* 2014).

Recent developments of techniques to analyse weather surveillance radar (WSR) measurements have provided insight into migratory behavior at unprecedented spatiotemporal scales (Kelly *et al.* 2012; Buler & Dawson 2014; Shamoun-Baranes *et al.* 2014). The magnitude of bird density on the ground is positively correlated with reflectivity (electromagnetic radiation reflected from birds in the radar beam) at the *en masse* initiation of migratory departures (exodus), typically close to dusk (Buler & Diehl 2009; Buler *et al.* 2012). To study the influence of geographic and ecological drivers of stopover incidence among nocturnal land-bird migrants across the northeastern U.S., we quantified seasonal-mean reflectivity during autumn migration using 7 years of measurements from 16 Doppler WSR stations (see Methods and Buler & Dawson 2014). Autumn migration involves higher numbers of migrants than in the spring, predominated by naïve juveniles more prone to disorientation and potential attraction to skyglow of cities *en route* (Ralph 1981; Gauthreaux & Belser 2006).

To disentangle anthropogenic and landscape-related factors affecting stopover density, and thereby assess whether artificial light at night might be affecting selection of stopover habitat, we estimated responses in seasonal-mean reflectivity to geographic, land cover and anthropogenic predictors using additive regression models fit by gradient boosting, a machine-learning technique (Hastie *et al.* 2009; Maloney *et al.* 2012). Appropriate spatial scales (Holland *et al.* 2004) between 1- and 50-km radii were identified for 13 predictor variables, including fractional land cover and artificial light effects. Artificial light at night (hereafter, ‘artificial light’) was quantified as the ratio of artificial to natural nocturnal light levels, i.e. a value of zero represents a sky devoid of anthropogenic light pollution (Falchi *et al.* 2016). Because migrants could potentially be diverted temporarily towards bright light sources before choosing more suitable stopover habitat nearby, we also considered distance to the nearest bright light source (based on artificial light > 5 within 1 × 1-km grid cells). To test whether our model could successfully distinguish among responses to the regional predictors – some of which were strongly inter- and spatially auto-correlated – we performed both model evaluation using a simulation-based approach with synthetic data for stopover density (Beale *et al.* 2010), and sensitivity analysis on key model parameters.

MATERIAL AND METHODS

Processing radar data

We sampled terrestrial distributions of migrating birds using WSR data obtained from the National Centers of Environmental Information (<https://www.ncdc.noaa.gov/nexradinv/>) for 16 radar stations throughout the northeastern U.S. during 7 autumn migration seasons (15 August–7 November, 2008–2014). For each suitable night of bird migration (outlined below) we interpolated a single ‘instantaneous’ radar volume scan (*sensu* Buler & Diehl 2009 and Buler & Dawson 2014) near the onset of well-synchronized *en masse* flights that generally occur near the end of evening civil twilight (i.e., sun angle 6° below horizon) (Åkesson *et al.* 1996). This approach minimizes displacement and dispersion of birds aloft from their ground sources, necessary to correctly identify the underlying stopover habitat of departing migrants. As further improvement to previous studies, we accounted for spatiotemporal variability in the precise timing of the onset of migration across the region by interpolating, for each night and within each radar domain, the precise sun angle at the peak of exodus flight (i.e., when the rate of change in reflectivity during exodus reaches its maximum). Specifically, we temporally-interpolated a spline function to the mean reflectivity within 10- to 40-km of the radar based on sun angles of 1.5° to 10° below the horizon (at intervals of 0.5°), and identified peak exodus as the instant of maximum growth rate (steepest slope) in reflectivity for each sampling night and radar, or 15 min after the *en masse* initiation of migratory flight, whichever occurred first (for most nights, the time of peak flight exodus occurred within 10 min of the initiation of flight).

Following established methods (Buler & Diehl 2009; Buler & Dawson 2014), we then accounted for how the radar beam systematically samples increasing heights with distance to derive a vertical profile of reflectivity (VPR), which is a function that describes the ratio of the mean reflectivity at a given height to the mean reflectivity in the entire airspace from the ground to 1.75 km above the ground within the radar domain. To extrapolate the mean reflectivity factor of birds to the entire (partially unmeasurable) column of airspace, we first divided the time-interpolated reflectivity at exodus within each sampled volume (i.e. along a 0.5° axial segment) by the mean VPR ratio along that axial segment. We then integrated this over the sampled height of 1.75 km, with further conversion of units, to produce the more biologically-meaningful measure of two-dimensional vertically-integrated reflectivity (VIR), which represents total reflected cross-sectional area of birds within a one-hectare vertical column ($\text{cm}^2 \text{ha}^{-1}$).

Because we were especially interested in spatial variability of typical (seasonal) stopover density, we avoided spatial biases by carefully screening and selecting nights where the entire radar domain was both precipitation-free and indicative of bird-dominated as opposed to insect-dominated migration; these were identified on the basis of mean airspeeds derived from azimuthal velocity and North American Regional Reanalysis wind measurements (Mesinger *et al.* 2006; Buler & Dawson 2014). In this way, we prioritized spatial as opposed

to temporal contiguity among radar domains. A total of 1491 nights (16% of sampled nights) were selected among the 16 radar stations. Nearly half of the nights (47%) were excluded due to the presence of precipitation at dusk, which moreover typically involve much lower migration density (Richardson 1990). Other reasons for excluding sampled nights were anomalous propagation of the radar beam (13%), contamination from non-precipitation sources such as clutter from sea breezes (8%), insect dominated flight activity (7%, i.e., about one-half of the number of bird-dominated nights), no or extremely sparse bird flight activity (5%), or missing or unusable data in the archive (3%). Any insect ‘contamination’ when birds are the dominant biota in the airspace would contribute little to the reflectivity signal, as larger reflectors tend to obscure the reflectivity signal of weaker reflectors (Stepanian *et al.* 2016). The extent of bat migration contributing to radar reflectivity is unknown, but likely minimal since only a handful of bat species migrate through the region, compared with hundreds of nocturnally migrating bird species.

To facilitate analysis, we divided the region into 628 603 1×1 -km grid cells. In addition to the temporal sampling described above, we further selected grid cells where at least 75% of nights sampled were based on reasonably complete vertical profiles (VPRs with 10% or greater coverage). Despite the conservative selection procedure, the resulting 166 296 1×1 -km grid cells used for analysis covered nearly a third (32%) of the northeastern U.S. and represent, to the best of our knowledge, an unprecedented spatial resolution and coverage in regional bird migration research.

Variable selection

To ensure that the model assessed stopover density on typical as opposed to extreme migration nights, we considered mean log-transformed VIR pooled over the 7-season period as the independent variable (this is equivalent to considering geometric mean in VIR, which under-emphasizes extreme values). Log-transforming also meant that predicted stopover density depended proportionally rather than additively on the responses to each predictor. To further alleviate the possibility of extreme values biasing estimated means where cells are under-sampled, we truncated mean VIR values below $0.01 \text{ cm}^2 \text{ ha}^{-1}$ (0.005% of data) and above $5 \text{ cm}^2 \text{ ha}^{-1}$ (0.16% of data).

Including spatial components explicitly as predictors can be important in spatial modelling (Beale *et al.* 2010; Maloney *et al.* 2012). Modelled stopover density was therefore allowed to vary explicitly with geographic location in addition to with proximate (landscape scale) factors, i.e. to allow predicted increases in stopover density (e.g. with increasing forest cover) to be higher in regions where migrant density was expected to be higher for other reasons (e.g. near coastlines).

Landscape influences on stopover can act at multiple spatial scales; for example, broad-scale availability of deciduous forest is associated with fine-scale migrant landbird stopover density (Buler *et al.* 2007). We considered fractional land cover of the following predictors within a series of landscapes ranging from 1- to 50-km radius from each 1×1 -km grid cell: deciduous and coniferous (evergreen) forest, agricultural, emergent

marsh, and developed (urbanized) cover. These land cover types were derived from the National Land Cover Database measured at 30-m resolution (Homer *et al.* 2015). Fractional cover was computed only for areas not covered by water. We also considered seasonal mean and standard deviation of the normalized difference vegetation index (NDVI) aggregated from measurements taken at 16-day intervals and 250-m resolution. These data were collected by the Global Moderate-resolution Imaging Spectroradiometer (MODIS) for each season and downloaded as product MOD13Q1 ver. 5 from the Land Processes Distributed Active Archive Center (<https://lpdaac.usgs.gov>).

To quantify attraction to nocturnal light sources, we used a dataset of the ratio of zenith artificial sky luminance to natural sky brightness as a measure of artificial light at night. The dataset was computed by Falchi *et al.* (2016) by compiling data from the Visible Infrared Imaging Radiometer Suite Day/Night Band sensor on the Suomi National Polar-orbiting Partnership satellite over 6 months during 2014 (no comparably precise and self-consistent dataset exists for the other study years, but regional patterns should remain overall similar during the study period). Artificial light at each data pixel (spatial resolution of 742 m) was obtained by integrating the contribution of the light arriving from sources up to a distance of 195 km, accounting for both direct upward and low-angle emission. We integrated these artificial light data over our 1-km spatial grid (using area-weighted means within cells) and calculated distance to the nearest bright light source, defined as 1-km pixels with artificial light ratios between 2 and 10.

To reflect the general path of broad-front migration and regional topography (*sensu* Farnsworth *et al.* 2016), we rotated the geographic axes clockwise by 42° , resulting in two predictors in UTM coordinates: X, southeastwards towards the Atlantic coast (i.e., perpendicular to the mean track direction of migratory flights) and Y, southwestwards along the coast (i.e., parallel to the mean track direction of migratory flights). To emphasize the local scale of coastal effects (typically within 50 km, e.g. LaFleur *et al.* 2016; Buler & Dawson 2014), we included distance to the Atlantic coast (dAtl) as predictor, set to a maximal value of 150 km (equivalent to the horizon distance from a height of 1500 m, a reasonable maximal flight altitude over land; e.g. La Sorte *et al.* 2015). The Spearman correlation between X and dAtl was 0.78. Finally, the corrective term dRdr was included to accommodate any lingering bias in reflectivity with distance to the radar.

We expected, and preliminary analyses revealed, that these four ‘geographic’ predictor variables (X, Y, dAtl, dRdr) exerted a dominant influence on mean reflectivity. Therefore, to identify appropriate spatial scales of the land cover and artificial light predictors, we chose for each predictor the spatial scale (between 1- and 50-km) that exhibited the largest absolute value Spearman Correlation coefficient with the residuals of a purely spatial model based on the four geographic predictors (and first-order interactions between X and Y). All land cover types exhibited the strongest (positive or negative) correlation with model residuals at a 1-km radius landscape scale (Fig. S1), except for artificial light and evergreen forest (both at a 2-km radius). Among land cover

predictors, the only highly correlated predictors ($R^2 > 0.5$) were artificial light with fractional cover of developed landscape (Spearman $R^2 = 0.83$). Among candidate definitions for distance to bright light, defining bright light as minimally 5 times natural values (*c.* 870 $\mu\text{cd}/\text{m}^2$) resulted in the highest correlation with residuals (Spearman $R^2 = 0.04$). This intensity of artificial light renders for example the Milky Way invisible to the human eye (Falchi *et al.* 2016). Artificial light ratios were also strongly negatively correlated with distance to bright light defined as above (Spearman $R^2 = -0.77$).

Model choice

We followed a machine-learning approach using Boosted Generalized Additive Models (package BGAM) in MATLAB 2015a (The Mathworks 2016) involving up to 20 000 iterative boosts based on steepest-gradient descent to minimize model deviance (Hastie *et al.* 2009; Maloney *et al.* 2012). The model divided the data into 7 cross-validated folds, and during each boosted iteration a step function based on a single predictor was chosen, based on maximum likelihood, to minimize deviance. To reduce bias and over-fitting, 10% of the data in each fold was randomly sampled at each iteration (*i.e.*, stochastic boosting), boosted iterations were updated using a low learning rate or step size (0.075) and the model was stopped before convergence (*i.e.* before successive iterations failed to reduce deviance), as a ‘shrinkage’ effect (Hastie & Tibshirani 1990; Maloney *et al.* 2012). Results were assessed by predictor influence, calculated as the reduction in model deviance attributable to each predictor, and by modelled response in mean reflectivity to each predictor. Model influence of a given predictor therefore reflects its importance in accounting for regional variability in stopover density, which will depend on both the regional variability of the predictor itself and the strength of the response to variation in that predictor. For depiction purposes, model responses (which were based on step functions) were smoothed using a moving average (MATLAB routine ‘smooth’) based on 5% of the data.

Model evaluation with synthetic data

Confronting spatial models with synthetic data is an important tool in assessing model robustness to autocorrelative effects and violations of model assumptions (see *e.g.*, Beale *et al.* 2010), and can moreover test a model’s ability to distinguish among responses to closely correlated predictors. Therefore, we tested model performance in distinguishing between responses to closely correlated anthropogenic effects (artificial light, distance to bright light and developed land cover) by designing synthetic stopover density datasets which included spatially autocorrelated noise, and also depended on other landscape and geographic predictors, some of which were excluded as model predictors (see Supporting Information and Equations S1 and S2).

Sensitivity analysis

Finally, we performed sensitivity analysis on the BGAM model (using observed reflectivity measurements) by

comparing results when (1) defining bright light sources as being at least 4 or 6 times greater than natural nocturnal levels, (2) adding deciduous forest at 50-km landscape scales as a predictor (to account for any diffusion of stopover density in forest-rich areas, *e.g.* far from bright light sources; see Fig. 2) and (3) varying the number of iterative boosts from 5000 to 40 000.

RESULTS

Seasonal mean reflectivity of birds emigrating from terrestrial habitats at the onset of nocturnal flights, a proxy for stopover density, exhibited strong variation among and within radar domains throughout the study region (Fig. 1). Patterns in mean reflectivity were visually discernible both among and within radar domains, *e.g.* relating to distance from the radar station (indicating measurement bias) and distance to coast (a biological effect) (Table 1).

The broader spatial distributions of artificial light and deciduous forest cover reveal that, if birds were to stop over near bright light sources, it would also reduce the incidence of forest cover they encounter (Fig. 2). Over most of the region, artificial light was typically lower (median 90% lower) than natural light levels but also exceeded natural levels, particularly near large cities along the Atlantic coast (Fig. 2a). Bright light was typically not too far away: while less than 1% of the region was brighter than 5 times (maximally 18.9 times)

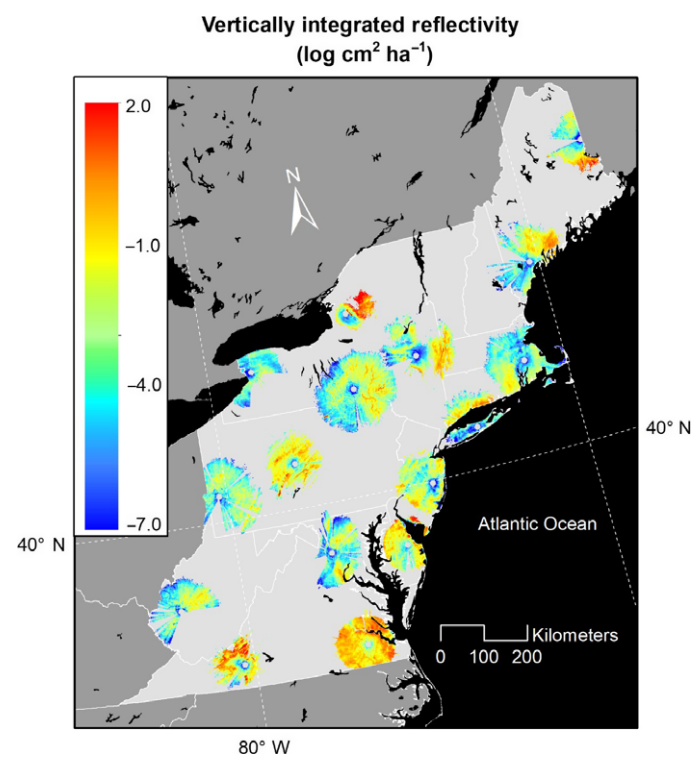


Figure 1 Regional patterns of migrant stopover density estimated via Weather Surveillance Radar (WSR). Autumn mean vertically-integrated reflectivity ($\log \text{cm}^2 \text{ha}^{-1}$) of migratory birds at nocturnal flight exodus among 16 WSR stations in the northeastern U.S. 2008–2014. The study area is depicted in light grey, water bodies in black and state boundaries in white.

Table 1 Names, descriptions and predictor ranges among 1×1 -km grid cells with radar measurements

Abbreviation	Description [units]	Range
NDVI	Mean autumn NDVI within 1 km	-0.01 to 0.84
NDVStd	Standard deviation NDVI within 1 km	0–0.26
Deciduous forest cover	Fractional deciduous forest cover within 1 km	0–1
Evergreen forest cover	Fractional evergreen forest cover within 2 km	0–1
Agricultural cover	Fractional agricultural cover within 2 km	0–1
Emergent marsh cover	Fractional emergent marsh cover within 1 km	0–1
Developed land cover	Fractional urbanized cover within 1 km	0–1
Artificial light	Ratio artificial:natural light intensity within 2 km	0.01–19
X	Location along NW to SE axis [m]	$4.1 \cdot 10^3$ – $6.7 \cdot 10^5$
Y	Location along NE to SW axis [m]	$3.2 \cdot 10^4$ – $1.6 \cdot 10^6$
dBrL	Distance to artificial light > 5 [km]	0–256
dAtl	Distance to Atlantic coast [km]	0–150
dRdr	Distance from radar [km]	1–101

natural levels, 60% of the region was within 100 km of such a bright light source (Fig. 2b). Incidence of deciduous forest was skewed in relation to distance to bright light (Fig. 2c); for example, beyond vs. within 100 km of bright sources, mean fractional deciduous forest cover was 35% higher (0.65 vs. 0.48, Wilcoxon Ranked Sum test: $Z = -237$, $P < 0.0001$). Mean vegetation productivity (as measured by NDVI) was however only marginally higher beyond vs. within 100 km of bright light (0.70 vs. 0.68, Wilcoxon Ranked Sum test: $Z = -101$, $P < 0.0001$).

When fitted to the reflectivity data, the model revealed clear patterns and hierarchies in how stopover density varied with predictors. Table 2 lists the model influence, i.e., reduction in deviance attributable to each predictor. As we expected, model influence was dominated by the broad-scale geographic predictors, with the spatial components (X and Y), distance to the radar and distance to the Atlantic coast accounting for 85% of model influence. Fig. S2 depicts a map of the modelled contribution to stopover density of these geographic predictors explicitly. Among landscape and anthropogenic predictors, deciduous forest cover was far and away the most influential (9% influence; see Table 2). Artificial light effects (distance to bright light and artificial light) were more influential (together 3%) than non-deciduous natural land cover (together 1%, including 0.2% from developed land cover). Mean and variability in NDVI were also moderately influential among landscape-scale factors (together 2%).

The modelled responses (Fig. 3) indicate that local stopover density varied with deciduous forest cover and the ‘anthropogenic’ predictors (distance to bright light, artificial light and developed land cover) by up to 70% (Fig. S3 depicts responses to all other landscape predictors and the corrective factor dRdr). Stopover density increased monotonically (up to 40%) with increasing deciduous forest cover (Fig. 3a) and decreased sharply (up to 50%) with increasing intensity of artificial light (Fig. 3b). Contrastingly, stopover density decreased steadily (up to 70%) with distance from bright light sources (Fig. 3c), particularly beyond 50–100 km. Taken together, the broad-scale response prevailed; for example, since median artificial light ratios within and beyond 100 km of bright light were 0.34 and 0.08, respectively, the local response to artificial light predicts *c.* 13% decrease in density within 100 km (Fig. 3b), but a simultaneous *c.* 50% increase due to distance to bright light effects (Fig. 3c). Increasing developed land cover caused a steady rise (by up to 20%) in stopover density (Fig. 3d). Among responses to the other predictors (Fig. S3), density showed sharp increases at both extremely vegetation-rich locations (response to NDVI, Fig. S3g), and within 25 km of the Atlantic Coast (Fig. S3d).

Model evaluation using synthetic data including spatially auto-correlated noise revealed (see Supplementary Information), as long as spatial components were included explicitly as predictors, that our boosted modelling approach could – in principle – successfully distinguish between responses to highly

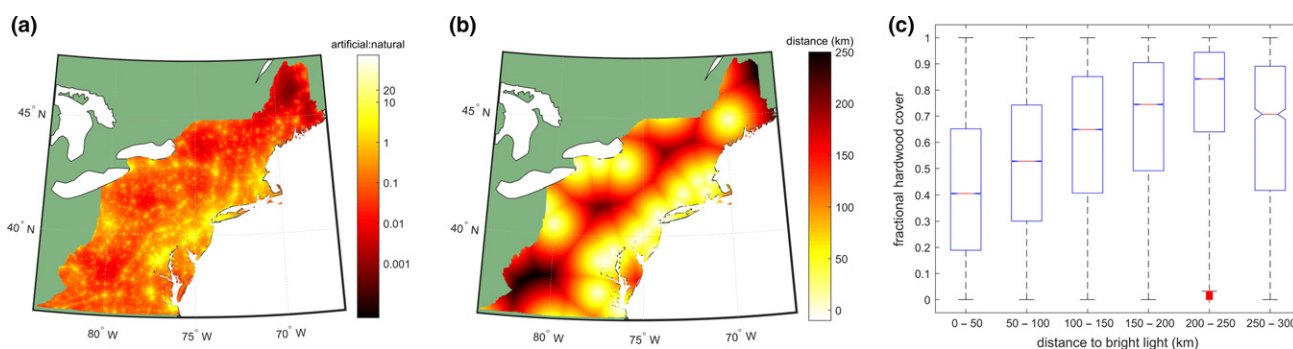


Figure 2 Regional characteristics of artificial light at night (artificial light) and distance to bright sky sources (distance to bright light), and their relation with forest cover. Contours, with levels on right-hand sides, of (a) magnitude of artificial light relative to natural nocturnal brightness levels, (b) distance (km) to bright light sources above $5 \times$ natural levels, and (c) boxplots depict an increase in the mean fraction of deciduous forest land cover with increasing distance to bright light.

Table 2 Model influence among the predictors, defined as percentage reduction in sum of squares deviance attributable to each predictor

Predictor	Model influence
X, Y and interactions	65.4
Distance to radar	18.2
Deciduous forest cover	9.1
Artificial light at night	1.9
Distance to Atlantic coast	1.7
Distance to bright light	1.2
NDVIstd	1.1
NDVI	0.8
Emergent marsh cover	0.3
Developed land cover	0.2
Agricultural land cover	0.2
Evergreen forest cover	0.1

correlated regional predictors, including to developed landscape and artificial light data (Figs S4–S8).

The sensitivity analysis, based on the observed reflectivity data, revealed robustness overall in predictor responses, including to distance to bright light. Total explained model deviance (D^2) increased only marginally (3%) when increasing the number of iterative boosts from 10 000 to 40 000 (Table S1). Modelled responses to predictors (Figs S9 and S10) were insensitive to the specific level of light intensity used to define bright light sources relative to natural nocturnal levels (the response curve of distance to bright light varied slightly, but always predicted higher density closer to bright lights). Lastly, when adding deciduous forest cover within 50 km to account for migrant and habitat density, the response functions (Fig. S11) for all other predictors remained consistent with the original responses (Fig. S3), despite the new predictor accounting for 33% of model influence among non-geographic predictors.

DISCUSSION

Our study demonstrates the utility of weather surveillance radar to assess the dynamic and multiscale nature of migrant bird stopover density, using multi-year measurements across a broad region and involving millions of birds. Within this

dynamic and multiscale context, with forest cover and proximity to the coast as primary drivers of stopover density (c.f. Buler & Dawson 2014), we provide novel evidence that artificial light at night affects aggregate stopover habitat use by migrating birds in complex ways at both regional and local scales.

We found a monotonic decrease in departing bird densities with increasing distance from bright light sources, extending out to the maximum distance within the region (250 km). This suggests, as postulated by Bowlin *et al.* (2015), that birds are drawn to these unintentional beacons during migratory flight at a broad scale. Moreover, our results validate experimental evidence that caged migratory birds orient towards the sky-glow of cities (Gauthreaux 1982). Contrastingly, but to a lesser degree (see Results and Fig. 3), lower emigrant density coincided with higher artificial light intensity at a finer (2-km radius) scale, indicating birds likely avoided bright areas as stopover sites during initial landfall or subsequent movements before their next nocturnal migratory flight (Chernetsov 2006; Cohen *et al.* 2012).

On the one hand, several additional factors may have contributed to the decrease in density in locally bright areas: (1) any increase caused by artificial light effects in the prevalence of post-landfall movements outside peak exodus (e.g. Mills *et al.* 2011; Van Doren *et al.* 2015), (2) any local delay in peak exodus caused by strong artificial light (we assumed uniform timing within radar domains on a nightly basis) and (3) increased mortality at bright locations (e.g. through collisions with structures). However, to the best of our knowledge, no effect of artificial light on post-landfall movements or subsequent timing of peak exodus has been noted, and mortality presumably cannot account for the predicted two-fold decrease between the darkest and brightest grid cells (Fig. 3b).

On the other hand, the broad-scale concentration of migrant density close to bright light sources would if anything be underestimated by any overestimation of the local influence of artificial light. The model evaluation supported the model's ability to successfully distinguish between dependences on artificial light and developed land cover (or a lack thereof), even though these predictors were highly correlated (see Supporting Information). Additionally, our explicit modelling of

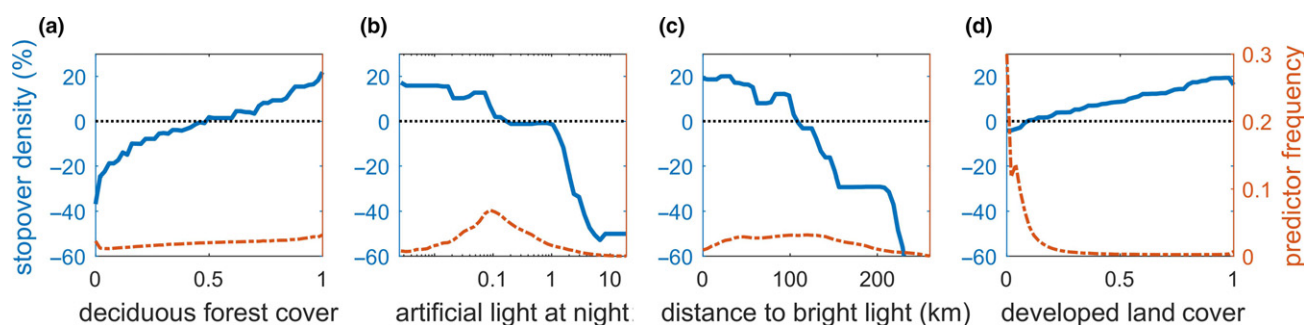


Figure 3 Modelled responses in autumn mean migrant stopover density (solid blue lines), indicating marginal change (%) in vertically-integrated reflectivity, as a function of (a) deciduous forest cover (the most influential landscape predictor) and three anthropogenic predictors: (b) artificial light at night, (c) distance to bright light (km) and (d) developed land cover. Responses are presented in descending order of model influence. Frequency distributions of predictor values are depicted by red dot-dashed lines (right-hand y-axis). Figs S2–S3 in the Supporting Information depict responses to geographic and other landscape-scale predictors.

distance to the radar presumably prevented any possible bias with distance to bright lights (e.g. should the radars under-sample reflectivity in remote and coincidentally forest-rich habitat).

We therefore suggest that artificial light and distance to bright light effects may exert a stronger influence on stopover density than other (urban) factors, i.e. associated with developed land cover (Buler & Dawson 2014; Zuckerberg *et al.* 2016), both in terms of prevalence across the region (as indicated by model influence) and magnitude of the response in stopover density. Our results are consistent with recent evidence from citizen science data that higher levels of diurnal bird abundance in urban areas during migration are associated with artificial light, especially when juveniles are undertaking their first migration journey in autumn (La Sorte *et al.* 2017). We note also that unlike ground-based visual survey methods, which provide an index of total bird use days of stopover areas (i.e., can be confounded by stopover duration), our radar sampling technique provides an index of total number of migrants by enumerating the biomass of birds as they leave stopover areas.

Therefore, artificial light evidently affects nocturnal migrants more ubiquitously than through collisions with structures near bright light sources, already cited as being a conservation concern among both migrating landbirds and seabirds (Gehring *et al.* 2009; Longcore *et al.* 2013; Loss *et al.* 2014; Rodríguez *et al.* 2015). Recent research indeed reveals that high intensity light sources like the Tribute in Lights display in New York City can have far-reaching (up to 5 km) impacts on migrating birds (Van Doren *et al.* 2017). However, the resulting effects on migrant fitness from each of these influences remain unresolved using our remote-sensing approach. Attraction to artificial light could compromise fitness through (1) migrants stopping over in landscapes with reduced forest cover, resulting in lower food abundance and reduced refuelling rates (Buler *et al.* 2007; Ktitorov *et al.* 2008), and thereby migration speed (Alerstam 2011; McLaren *et al.* 2013), (2) alternatively, affected birds searching longer for suitable habitat (e.g. with greater forest cover) away from bright areas, incurring extra time and energy expenditure and increased risk of encountering hazards (Robson & Barriocanal 2008; Legagneux *et al.* 2012; Cohen *et al.* 2014), (3) heightened anthropogenic mortality risks, e.g. from collisions with structures or vehicles, cat predation, and poisoning (Loss *et al.* 2013, 2014). More encouragingly, while the extent to which migrants are able to effectively exploit developed landscapes remains relatively unknown (Seewagen & Slayton 2008; La Sorte *et al.* 2014), the heightened predicted density at locations with exceptionally high seasonal mean NDVI (Fig. S3g) may attest to the ability of migrants to select stopover habitat based on food availability more strongly than on simple land cover (Buler *et al.* 2007).

In the face of ongoing habitat destruction, urban development, and associated anthropogenic light pollution, we recommend that future research should attempt to quantify how and under which conditions artificial light affects the stopover process – and resulting effects on individual migrants and populations. Identification of important and sensitive

migratory regions (Mehlman *et al.* 2005; Buler & Dawson 2014) and establishment of energy-efficient policies that reduce artificial night lighting (Elvidge *et al.* 2014) could both promote the safety of migrants (Gehring *et al.* 2009) and reduce artificial light effects on migratory stopover. Given the clear artificial light effects evident in the weather radar measurements, such policies may together prove important in conserving migratory populations at continental scales and across assemblages of migratory taxa during one of the most vulnerable life-history stages.

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AUTHORSHIP

JJB, JDM, DKD, ELW designed the study. JJB, TS, JAS, MB wrote software and processed radar data. JAS and JJB compiled predictor datasets. JDM and EvL wrote software, and performed model analysis (JDM) and evaluation (JDM, EvL). JDM and JJB wrote the manuscript with input from all co-authors.

DATA ACCESSIBILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.18v5d>.

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