








## LETTER

# A place to land: spatiotemporal drivers of stopover habitat use by migrating birds

Emily B. Cohen,<sup>1\*</sup>  Kyle G. Horton,<sup>2†</sup>  Peter P. Marra,<sup>1‡</sup>  Hannah L. Clipp,<sup>3§</sup>  Andrew Farnsworth,<sup>2</sup>  Jaclyn A. Smolinsky,<sup>3</sup> Daniel Sheldon<sup>4</sup>  and Jeffrey J. Buler<sup>3</sup> 

### Abstract

Migrating birds require *en route* habitats to rest and refuel. Yet, habitat use has never been integrated with passage to understand the factors that determine where and when birds stopover during spring and autumn migration. Here, we introduce the stopover-to-passage ratio (SPR), the percentage of passage migrants that stop in an area, and use 8 years of data from 12 weather surveillance radars to estimate over 50% SPR during spring and autumn through the Gulf of Mexico and Atlantic coasts of the south-eastern US, the most prominent corridor for North America's migratory birds. During stopovers, birds concentrated close to the coast during spring and inland in forested landscapes during autumn, suggesting seasonal differences in habitat function and highlighting the vital role of stopover habitats in sustaining migratory communities. Beyond advancing understanding of migration ecology, SPR will facilitate conservation through identification of sites that are disproportionately selected for stopover by migrating birds.

### Keywords

Florida, Gulf of Mexico, migration, nearctic-neotropical migratory bird, NEXRAD, weather surveillance radar.

Ecology Letters (2021) 24: 38–49

## INTRODUCTION

Worldwide, trillions of animals make spring and autumn migrations across continents. Long-distance migrations are accomplished through alternating phases of movement: passage, during which the energetic reserves are depleted, and stopovers, during which the energetic reserves are replenished (Nathan *et al.*, 2008). Both of these phases contribute to the success of the migratory journey and are under strong natural selection pressure (Hedenström, 2008). Intercontinental bird migration is often characterised by nocturnal flights and diurnal stopovers with most of the duration of the migratory journey spent at stopover sites (Hedenström and Ålerstam, 1997; Ålerstam, 2003), where the quality of the habitat can influence the subsequent flight range (Bayly *et al.*, 2013; Gómez *et al.*, 2017). Access to food-rich stopover habitat for refuelling may vary between seasons and has consequences for the duration of the migratory period and subsequent survival and reproduction (Lindström, 1990; Hedenström, 2008; Paxton and Moore, 2017). Therefore, the spatiotemporal factors that determine where and when a bird makes a stopover are fundamentally important to the biology of migratory birds.

The numbers of migrating birds using a habitat patch during a spring or autumn day are functions of the overall magnitude of migration through that area, for example, the number of birds passing through the airspace overhead, and the proportion of those birds that select that particular patch to stop. Recent work has elucidated much about the broad-scale seasonal passage of landbirds aloft (e.g. Nilsson *et al.*, 2019; Horton *et al.*, 2020) and the delineation of stopover densities in terrestrial habitats (e.g. Buler and Dawson, 2014; McLaren *et al.*, 2018), but we lack a holistic understanding of migration inclusive of passage and stopover and the processes by which migrating birds are filtered from airspace into terrestrial habitat. Here, we advance a more comprehensive approach to understanding migration by integrating broad-scale passage and stopover distributions for the first time to create the stopover-to-passage ratio (SPR), a quantitative measure of the percentage of passage migrants that stop in a given area. Beyond its value for migration ecology, we suggest that SPR will facilitate conservation through identification of sites that are disproportionately selected for stopover by migrating birds.

Filtering of migrants from flight to stopover is a hierarchical process influenced by multiple extrinsic factors, including

<sup>1</sup>Migratory Bird Center, Smithsonian Conservation Biology Institute, National Zoological Park, 3001 Connecticut Ave NW, Washington, DC 20008, USA

<sup>2</sup>Center of Avian Population Studies, Cornell Lab of Ornithology, 159 Sapsucker Woods Rd, Ithaca, NY 14850, USA

<sup>3</sup>Department of Entomology and Wildlife Ecology, University of Delaware, 531 South College Ave, Newark, DE 19716, USA

<sup>4</sup>College of Information and Computer Sciences, University of Massachusetts, Amherst, MA 01003, USA

\*Correspondence and present address:

Emily B. Cohen, Appalachian Laboratory, University of Maryland Center for

Environmental Science, 301 Braddock Rd, Frostburg, MD, 21532, USA. E-mail: Emily.Cohen@UMCES.edu

<sup>†</sup>Present Address: Fish, Wildlife, and Conservation Biology, Colorado State University, 1474 Campus Delivery, Fort Collins, CO 80523, USA

<sup>‡</sup>Present Address: Department of Biology and the McCourt School of Public Policy, Georgetown University, 37th and O St NW, Washington, DC 20057, USA

<sup>§</sup>Present Address: Division of Forestry and Natural Resources, West Virginia University, Morgantown, WV 26506, USA

atmospheric conditions (Shamoun-Baranes *et al.*, 2017) and availability of habitat (Buler and Moore, 2011; Moore, 2018), and multiple factors intrinsic to the migrant itself, including navigational abilities (Mouritsen, 2018), energetic reserves (Loria and Moore, 1990) and distance to destination (Jenni and Schaub, 2003; Paxton and Moore, 2017). At the broadest geographical scales, the numbers of migrating birds using a particular habitat patch could be a direct reflection of wind-driven flyways (Shamoun-Baranes *et al.*, 2017), although this has never been tested. Among landscapes, densities of birds in stopover habitat are positively related to the amount of forest cover (Buler and Moore, 2011; Lafleur *et al.*, 2016) and vegetation productivity (McLaren *et al.*, 2018), which may serve as cues to identify high-quality habitat prior to landing (Chernetsov, 2006; Buler *et al.*, 2007). Once on the ground, forest cover is related to food availability (Buler *et al.*, 2007), foraging behaviour (Cohen *et al.*, 2014), and refuelling rates (Kittorov *et al.*, 2008) of migrating birds. Nevertheless, a migrant with sufficient energetic reserves far from its destination and encountering weather favourable for flight, is likely to pass over even the highest quality landscapes to continue flight (Alerstam and Lindström, 1990; Gudmundsson *et al.*, 1991). Thus, characteristics of the migrants themselves, which are likely to vary between migration seasons, mediate the influence of landscape features on the decision to stop.

The patterns of where and when migrating birds stop during spring and autumn reflect variability in the drivers of the filtering process and how migrants use stopover habitats. For example, poor energetic condition and weather may concentrate migrants in the first available habitats along coastlines, irrespective of food resources, where they can rest and recover after making non-stop over-water flights (Gauthreaux *et al.* 2006; Lafleur *et al.*, 2016; Clipp *et al.*, 2020). Alternatively, migrants may concentrate in food-rich habitats to forage and build energetic reserves before making a non-stop flight (Buler *et al.*, 2007). Additionally, anthropogenic alteration of landscapes such as increasing levels of light pollution encountered during migration may alter the decision to stop (Van Doren *et al.*, 2017; Cabrera-Cruz *et al.*, 2018; McLaren *et al.*, 2018). Multiple interacting factors may constrain access to high-quality stopover habitats at broad scales, and those constraints are likely to vary between seasons.

The lack of a comprehensive characterisation of migratory passage and stopover habitat use represents a fundamental gap in our knowledge, primarily existing because of the methodological challenges in collecting broad-scale information about distributions of birds in terrestrial habitats during the day and in the airspace at night (Buler *et al.*, 2017; Cohen *et al.*, 2017). Analyses of data collected by weather surveillance radars bridge this gap, for example, at continental and decadal scales (Van Doren and Horton, 2018; Bauer *et al.*, 2019; Dokter *et al.*, 2019; Lin *et al.*, 2019). Moreover with systematic observations collected continuously during spring and autumn, radar data facilitate spatial and temporal assessments of paired airspace and stopover habitat use across entire migration corridors (Shamoun-Baranes *et al.*, 2014; Bauer *et al.*, 2019). No other approach offers such comprehensive and unbiased observations of migration patterns across multiple spatial scales over time (Kelly and Horton, 2016).

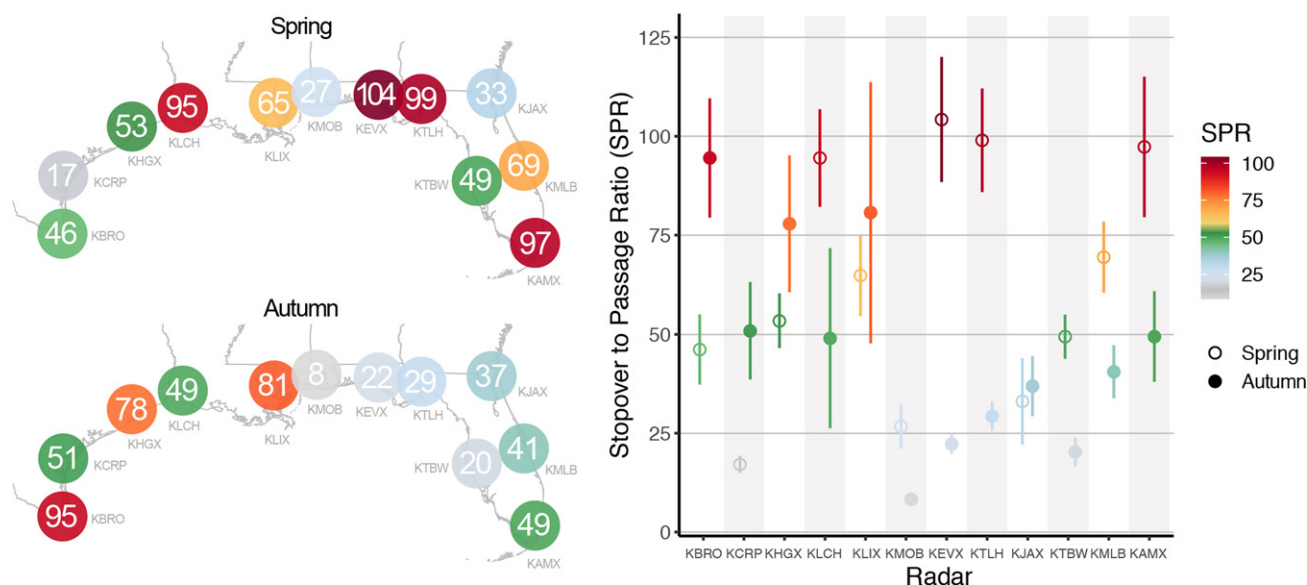
Our objectives were twofold. First, we assessed spatiotemporal patterns of SPR with complementary measures of stopover and passage density from 12 weather surveillance radars around the south-eastern US from southern Texas to southern Florida. We modelled variability in SPR in relation to season, geographical position and timing within season to determine the extent to which SPR followed the magnitude of migration: (1) between seasons, higher in autumn when passage densities increase with the addition of young of the year (Dokter *et al.*, 2018); (2) geographically, following wind-driven flyways (La Sorte *et al.*, 2016); and (3) within-seasons, highest at peak passage (Horton *et al.* 2019). Second, to understand the interplay of geographical and landscape features on stopover habitat use, we conducted the most comprehensive modelling effort of bird stopover distributions for any region globally in terms of geographic and temporal scope and consideration of predictors. We predicted that stopover density is: (1) higher close to the coastline in spring when birds are arriving after navigating the Gulf of Mexico or the Atlantic Ocean, as opposed to autumn when birds are moving south through the continent and have the ability to stop further inland (Buler *et al.*, 2007) and (2) higher in landscapes with greater forest cover and vegetation productivity in autumn when birds are building energetic reserves prior to navigating the Gulf of Mexico or the Atlantic Ocean, as opposed to spring when they may not have the ability to select among available habitats after long non-stop flights (Smolinsky *et al.*, 2013; Deppe *et al.*, 2015).

## METHODS AND MATERIALS

### Radar data processing

We obtained Level II radar volume scan data from the NOAA's National Climatic Data Center for spring (March–May) and autumn (August–October) of 2008–2015 from 12 radars located along the Gulf of Mexico and Atlantic coasts of the south-eastern US (Fig. 1). We used reflectivity factor, the amount of the returned electromagnetic radiation from birds in the air, to quantify aggregate bird biomass, and radial velocity, the mean target velocity relative to the radar, to discern birds from insects (Gauthreaux & Belser 1998). Because the number of stopover sampling days varied among radars, we measured nightly stopover and passage densities on the same nights. For each year of data, we calculated mean passage and stopover values on a biweekly interval during spring and autumn (first and second half of March, April, May, August, September and October).

For stopover distributions, we screened data following established methods (Buler *et al.*, 2017), visually examining each sampling night to retain radar scans dominated by birds and to exclude data within radar scans with strong beam blockage, located over open water or containing persistent ground clutter. Non-avian biological targets such as large numbers of insects in the airspace (Hu *et al.*, 2016), also prohibit measurement of migrating birds. We conservatively eliminated nights with mean animal airspeeds of less than  $5 \text{ m s}^{-1}$ , indicative of insect-dominated flights (Larkin, 1991; Cabrera-Cruz *et al.*, 2013). While bats cannot be distinguished from birds during movement through the airspace, 'roost



**Figure 1** Mean stopover-to-passage ratio (SPR), the percentage of passage migrants that stop within 37.5 km of each of 12 radars located around the US coastline of the Gulf of Mexico and Atlantic Ocean in Texas (KBRO, KCRP, KHGX), Louisiana (KLCH, KLIX), Mississippi, Alabama (KMOB) and Florida (KEVX, KTLH, KJAX, KTBW, KMLB, KAMX) during spring and autumn. Seasonal means (se) are across years (2008–2015) and biweekly periods and are weighted by the number of sampling nights per period.

rings' of bats are visible when they depart *en mass* for nocturnal flight (Stepanian and Wainwright, 2018). Therefore, we excluded data from areas around the Houston (KHGX) and Corpus Christi (KCRP) radars in Texas with persistent free-tailed bat (*Tadarida brasiliensis*) roosts (Horn and Kunz, 2008; Clipp *et al.*, 2020). Mapping the relative density of birds departing stopover habitat among radars requires an instantaneous measure of the density of migrating birds aloft during the onset of nocturnal flight for each sampled night. We used the time when bird density aloft reaches the maximum rate of increase (i.e. peak exodus) as our standard sampling time (McLaren *et al.*, 2018). However, the precise timing of peak exodus varies geographically and from night to night. Therefore, we determined the instantaneous sampling time of peak exodus separately for each radar-night. The radar beam propagates at a slight tilt angle (0.5°) and widens with distance from the radar. This change in the beam sampling heights above the ground with distance from the radar creates bias in reflectivity measures since birds are not uniformly distributed with height at the onset of flight (Buler and Diehl, 2009). To reduce this bias, we first derived a function that describes the vertical distribution of birds as the ratio of mean reflectivity at a given height relative to the mean reflectivity across all heights (i.e. 0–1750 m agl) for each radar-night following Buler and Dawson (2014). We then used this function, the vertical profile of reflectivity, to extrapolate reflectivity measured within the heights of each sampling volume to the mean cross-sectional area of reflectivity (i.e. bird biomass) expected within the entire vertical column from 0 to 1750 m above ground level in units of  $\text{cm}^2 \text{ km}^{-3}$ . We transformed this volumetric density measure into a surface density measure of bird biomass departing the ground at peak stopover exodus in units of  $\text{cm}^2 \text{ km}^{-2}$  (Chilson *et al.*, 2012). This measure (hereafter, stopover density) correlates positively with observed

bird stopover density on the ground from field surveys (Buler and Diehl, 2009). In total, we processed 1472 spring and autumn radar-nights, totalling 148 304 radar scans, over 8 years and 12 radars. Following the application of data filters, we quantified stopover densities for one or more radars on 78% of spring and 61% of autumn nights over the 8-year period, including 7–25% of sampling days from individual radars.

For passage density, we processed data at 30-min intervals from sunset to sunrise on the sampling days within each biweekly period. We used measures of radar reflectivity in units of  $\text{cm}^2 \text{ km}^{-3}$  (Chilson *et al.*, 2012) and constructed vertical profiles of mean migrant groundspeed and track direction at 0.1 km height bins by fitting a sine function to radial velocity by azimuth following (Browning and Wexler, 1968) and, when necessary, correcting radial velocities for velocity aliasing (i.e. when bird velocities exceeded the radar pulse repetition frequency) following Sheldon *et al.* (2013). We classified and removed weather contamination using MistNet (Lin *et al.*, 2019) and then constructed vertical profiles of mean reflectivity from 0 to 3 km above ground level in 0.1 km height bins from the five lowest elevation scans in 5–37.5 km around each radar (Sheldon, 2015; Horton *et al.*, 2020).

We multiplied profile measures of volumetric radar reflectivity by the bin height (0.1 km) to yield areal reflectivity of passage migrants aloft in units of  $\text{cm}^2 \text{ km}^{-2}$ . We restricted passage measures to those with northward track directions ( $< 90^\circ$  and  $> 270^\circ$ ) during spring and southward track directions during autumn ( $> 90^\circ$  and  $< 270^\circ$ ). Once the total passage was calculated for each altitudinal bin, they were summed to give the total passage. We calculated nightly passage rates for each altitudinal bin of the vertical profile by integrating the product of radar reflectivity ( $\text{cm}^2 \text{ km}^{-2}$ ) and migrant groundspeed ( $\text{km hr}^{-1}$ ) throughout the duration of

the night (hr), yielding units of  $\text{cm}^2 \text{ km}^{-1}$ ) (Horton et al. 2019).

### Calculating the stopover-to-passage ratio

For SPR, we derived corresponding measures of stopover and passage biomass as the total cross-sectional area of birds integrated through the night in units of  $\text{cm}^2$  within 5 and 37.5 km of the radar. We first multiplied the mean nightly stopover density ( $\text{cm}^2 \text{ km}^{-2}$ ) at the instant of peak migratory exodus among sampling volumes around each radar for each biweekly period by the land area within 37.5 km of each radar ( $\text{km}^2$ ) to get total biomass at the instant of peak exodus. When calculating mean biweekly stopover densities, we excluded individual measures of extremely high value (top 0.1%) that may be the result of unresolved clutter. To integrate the total biomass of birds departing stopover throughout the night, we divided the mean instantaneous stopover biomass at peak exodus by 0.10, which is the estimated cumulative proportion of nocturnal migrants aloft at the peak sampling time based on departure timing of individual radio-tagged species (Buler et al., 2017). We multiplied the total nightly passage density ( $\text{cm}^2 \text{ km}^{-1}$ ) by the length of the sampling transect (km) to get total passage biomass (Horton et al. 2019). Thus, SPR is the unitless ratio of biweekly means of the total stopover biomass divided by the total passage biomass for corresponding areas. We present the ratio as a percent with higher values indicating a larger proportion of birds stopping relative to the numbers passing through the airspace. While SPR should not theoretically exceed 100%, we did not constrain it to this maximum and it slightly exceeded 100% in a few cases due to measurement errors in the constituent values. We modelled SPR in a generalised linear mixed effects model to identify geographic and temporal differences (with a log link to keep estimates positive) by season, radar location (latitude and longitude) and time of season with the 'lme4' R package (Bates et al., 2015). We included all two-way interactions and year as a random effect with a varying intercept, and weighted the observations by the number of sampling days.

### Modelling the influence of geographic and landscape features on stopover distributions

While SPR is a single measure for each biweekly period over each radar at the extent of 37.5 km, we calculated stopover density at a finer resolution ( $1\text{-km}^2$ ) for all of the land area within *c.* 80 km of each radar (i.e. the range at which the radar beam passed over 95% of the vertical distribution of birds in the air) to model the relationship between stopover density and geographic and landscape features. We then applied those relationships to predict stopover density across the entire region. We limited predictions to those areas in-between radars (true interpolation) rather than to areas beyond the extent of the training data (extrapolation). We compiled predictive data for the entire coastline including areas not sampled by the radars. We created a grid of 427 513  $1\text{-km}^2$  cells covering the study area and populated individual cells with stopover density and predictor variables (Table 1). We

used a 2016 regional coastal landcover classification (NOAA, 2016) to estimate the proportion of water and six reclassified landcover types (hardwood, urban, agriculture, evergreen, scrub, wetland) within a  $5\text{-km}^2$  square window around each  $1\text{-km}^2$  cell. We included normalised difference vegetation index as a measure of vegetation productivity, collected by the MODIS Aqua sensor over 16-day periods (Huete et al., 2011). Because light pollution influences stopover habitat use (McLaren et al., 2018), we quantified the distance to bright light five times higher than the natural level ( $>63$  on a scale from 0 to 65; from NDMSP-OLS Nighttime Lights data for 2012) (NOAA, 2012). Because local weather conditions influence departure from stopover habitat (e.g. Åkesson and Hedenström, 2000; Schaub et al., 2004; Sjöberg et al., 2015; McCabe et al., 2018), we included mean temperature and winds (800–1000 mb) at the time of departure to control for the influence of local weather conditions. We extracted temperature and wind measures for the radar-nights included from NOAA's North American Regional Reanalysis dataset (Mesinger et al., 2006). We included two additional attributes to account for any residual range bias: distance from the radar and ground elevation relative to the radar antenna height. We ran separate models for each season including the year and biweekly periods. Many of the numeric predictor variables were moderately correlated ( $r > \pm 0.30$ ) but only distance to coastline and elevation relative to the radar were strongly correlated ( $r = 0.60$ ). We retained these variables because we were testing predictions about distance to coastline and relative elevation was corrective for range detection error.

We used boosted regression trees to fit complex nonlinear relationships with multiple interactions among predictors while avoiding over-fitting (De'ath 2007; Elith et al., 2008). We identified the optimal number of trees at which the average holdout residual deviance was minimised with the 'gbm.step' function within the 'dismo' R package (Hijmans et al., 2017). Models were specified with tree complexity = 18, learning rate = 0.2, bag fraction = 0.5, minimum number of trees = 25 per step and a Gaussian error distribution (Elith et al., 2008). The response variable for each time period was the log-transformed arithmetic mean of stopover density ( $\text{cm}^2 \text{ ha}^{-1}$ ). To reduce spatial autocorrelation, we independently ran 25 subset models for each season with data separated by 5 km and model-averaged the results. We computed predicted values of stopover densities for each  $1\text{-km}^2$  grid cell for each model and averaged responses across the 25 subset models and mapped the predicted biweekly and season mean distributions of stopover densities. Finally, we evaluated model fit with an assessment of the total deviance explained of training data and a mean cross-validation correlation. All analyses were conducted in R version 3.6.3 (R Core Team, 2020).

## RESULTS

### Stopover-to-passage ratio

We estimate that over half of birds migrating through the south-eastern US stop in coastal habitats during spring and autumn ( $\text{SPR} = 52.53\% \pm 2.42\%$ ). The magnitude of migration increased between spring and autumn, from

**Table 1** Names and ranges of predictor variables among the study area's 427,513 1-km<sup>2</sup> cells. Relative importance among predictors, defined as the percentage reduction in sum of squares deviance attributable to each predictor, and their order of importance for spring and autumn

Category	Predictor	Range	Relative importance		Importance rank	
			Spring	Autumn	Spring	Autumn
Temporal	Year	2008–2015	11.93	9.53	2	2
	Biweekly period	1 March–31 May, 1 August–31 October	9.60	5.05	3	9
Geographic	Longitude [°]	−80 to −98.5	15.20	14.81	1	1
	Distance from coast [km]	0–139	4.01	4.27	8	11
Landscape	Proportion evergreen *	0–1	2.38	8.39	17	3
	Proportion hardwood *	0–1	2.86	4.25	13	12
	Proportion wetland *	0–1	2.91	3.23	12	14
	Proportion agriculture *	0–1	2.79	3.14	14	15
	Proportion urban *	0–1	2.72	2.99	15	16
	Proportion scrub *	0–1	2.50	2.76	16	17
	Proportion water *	0–0.75	0.96	1.01	18	18
	Normalised Difference Vegetation Index	0–1	3.90	5.95	9	7
Weather <sup>†</sup>	Distance to light pollution [km]	0–114	3.05	3.36	11	13
	Temperature [K]	282–316	7.46	6.16	6	6
	Meridional (north/south) wind component [m/s]	−8.1 to 9.9	9.45	8.26	4	4
	Zonal (east/west) wind component [m/s]	−13.8 to 6.1	8.59	6.50	5	5
Corrective	Distance from radar [km]	0–186	6.01	5.91	7	8
	Ground elevation relative to radar antenna [m]	−0.46 to 32.1	3.66	4.44	10	10

\*Within 5 km.

<sup>†</sup>3 h after migration onset.

$9.54 \times 10^6 \pm 0.87 \times 10^6$  to  $24.62 \times 10^6 \pm 1.90 \times 10^6$  cm<sup>2</sup> for passage ( $F_{1,532} = 104.19$ ,  $P < 0.001$ ) and  $2.15 \times 10^6 \pm 0.08 \times 10^6$  to  $4.86 \times 10^6 \pm 0.24 \times 10^6$  cm<sup>2</sup> for stopover ( $F_{1,533} = 171.48$ ,  $P < 0.001$ ) while SPR followed the opposite pattern, declining from  $57.24\% \pm 3.12\%$  to  $43.66\% \pm 3.63\%$  between spring and autumn ( $F_{1,535} = 5.59$ ,  $P = 0.02$ ). The geographical magnitude of migration increased from the west to east in autumn and east to west in spring (passage  $F_{1,530} = 28.75$ ,  $P < 0.001$ ; stopover  $F_{1,531} = 9.29$ ,  $P < 0.001$ , Fig. 2) while SPR followed the opposite pattern, increasing west to east in spring and east to west in autumn (Longitude\*Season  $F_{1,535} = 12.57$ ,  $P < 0.001$ , Fig. 2). SPR was negatively related to the magnitude of migration in the east and was highest in the east in spring when passage and stopover densities were lowest (Fig. 2). Among radars, SPR varied more than 10-fold within and between seasons; it was highest in the spring in southern Florida, the Florida panhandle, and western Louisiana, and it was highest in the autumn in southern Texas (Fig. 1). SPR showed the least seasonal difference along the Atlantic coast through Jacksonville, Florida (KJAX, Fig. 1). Within seasons, SPR was lowest during peak migration and highest during the beginning and end of the season ( $F_{5,535} = 22.49$ ,  $P < 0.001$ ; Fig. 3).

### Geographical and landscape features drive seasonal stopover

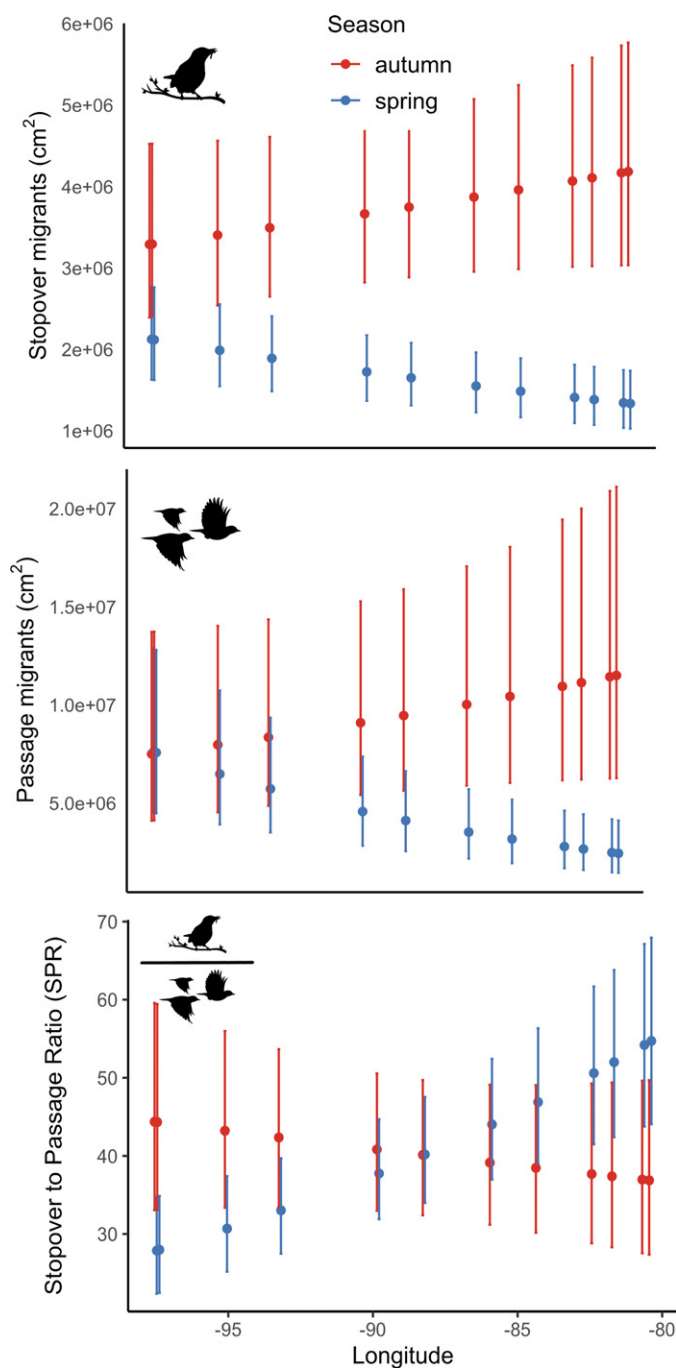
Geographical location was the strongest driver of stopover density, with longitude the most influential predictor during both spring and autumn (Table 1). Distance from the coastline was moderately more influential during spring (Table 1) when migrants concentrated in higher densities within 4 km of the coastline (Supporting information). Forest cover and

vegetation productivity positively influenced stopover density in both seasons (Supporting information) but the influence of forest cover on stopover density in autumn was twice that in spring, particularly evergreen forest cover (Table 1). Stopover density varied among years, with the highest densities in 2015 and the lowest in 2009, and within seasons, with strong within-season peaks during late April and early May and a more moderate peak during late September through early October (Table 1, Supporting information).

Models had a mean cross-validation correlation of  $0.77 \pm 0.002$  for spring and  $0.80 \pm 0.002$  for autumn. Region-wide interpolated maps demonstrated the west to east shift in stopover densities between spring and autumn and highlight stopover areas that are consistently used between seasons, particularly in parts of Texas, Louisiana and Florida (Fig. 4). These maps also revealed geographical variability in stopover densities within seasons. During spring, stopover densities in the panhandle of Florida peaked earlier than along the coasts of Texas and Louisiana while during autumn within season variability in stopover densities was fairly consistent across the region (Fig. 5).

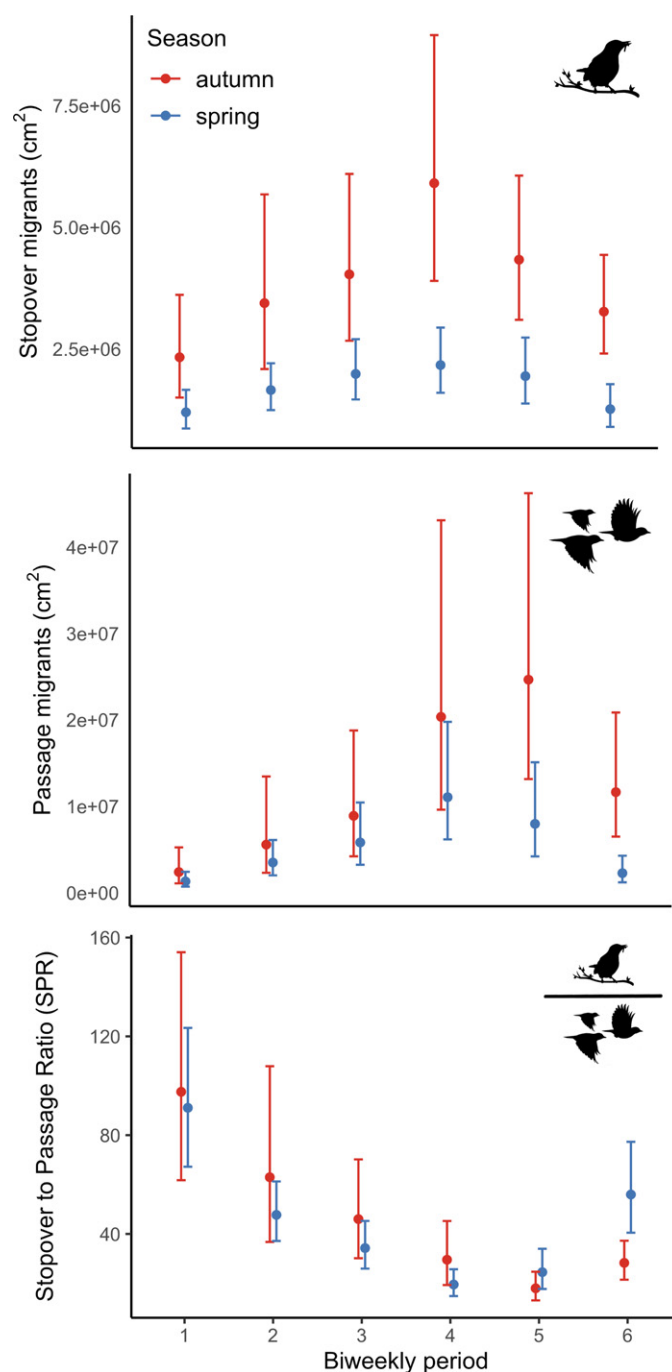
### DISCUSSION

Migration is one of the most poorly understood periods of avian life cycles. We fill a critical knowledge gap in the understanding of bird migration, linking alternating phases of passage (i.e. flights) and stopovers (e.g. foraging) in the most heavily trafficked North American migratory corridor (Cohen *et al.*, 2017). We found approximately half of the birds migrating through the Gulf of Mexico and Atlantic coasts of the south-eastern US stop within 100 km of its coastlines,



**Figure 2** Estimated marginal means  $\pm$  95% CI of corresponding mean passage density ( $\text{cm}^2$ ), stopover density ( $\text{cm}^2$ ) and the stopover-to-passage ratio (SPR) by longitude around 12 radars located around the Gulf of Mexico and Atlantic coasts of the south-eastern US during spring and autumn modelled across biweekly periods, latitude and years (random effect) and weighted by the number of sampling nights per period.

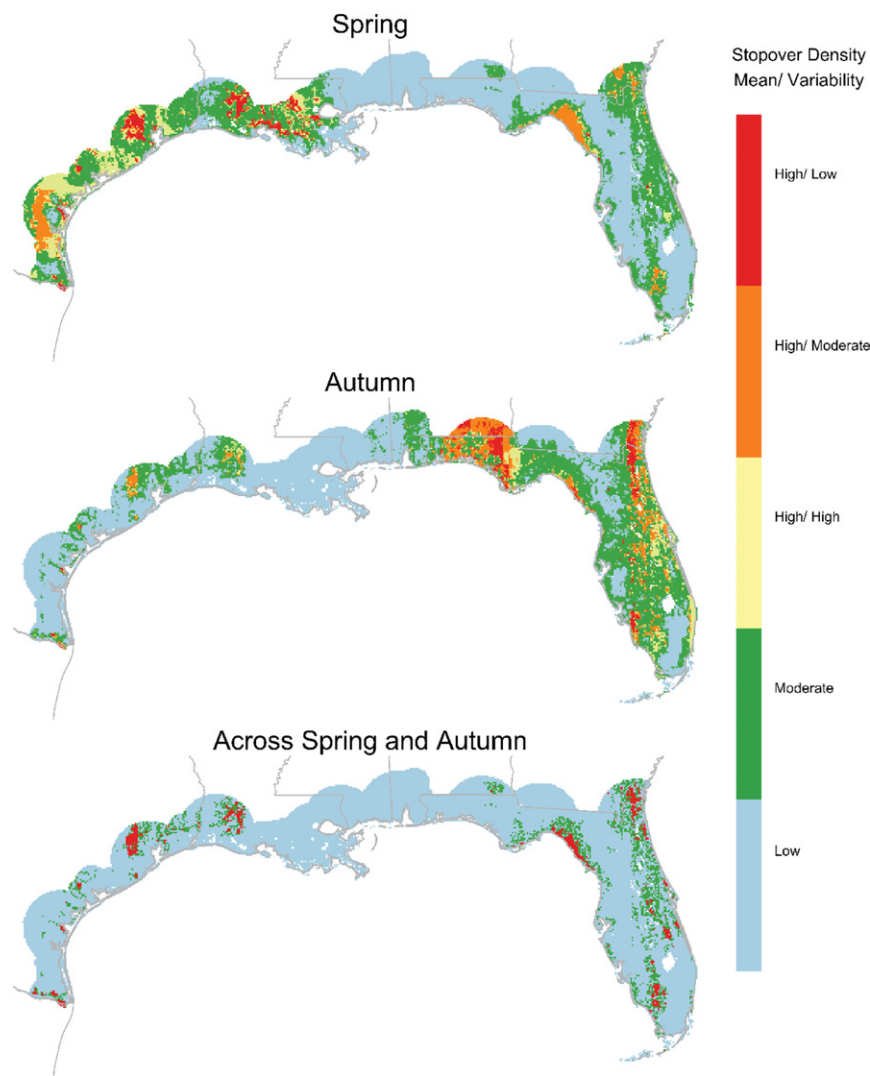
totalling *c.* 1.2 to 2.0 billion birds each spring and autumn (*sensu* Dokter *et al.*, 2018; Horton *et al.* 2019). In addition to quantifying the abundance of Nearctic-Neotropical birds that converge in these coastal habitats, we observed within and between-season differences in SPR and stopover densities that



**Figure 3** Estimated marginal means  $\pm$  95% CI of corresponding mean passage density ( $\text{cm}^2$ ), stopover density ( $\text{cm}^2$ ) and the stopover-to-passage ratio (SPR) around 12 radars located around the Gulf of Mexico and Atlantic coasts of the south-eastern US during biweekly periods of spring (March 1–15, March 16–31, April 1–15, April 16–30, May 1–15, May 16–31) and autumn (August 1–15, August 16–31, September 1–15, September 16–30, October 1–15, October 16–30) modelled across location and years (random effect) and weighted by the number of sampling nights per period.

reveal site selection and potential migratory bottlenecks where geography or restricted habitat may disproportionately concentrate birds along migration routes (Bayly *et al.*, 2018).





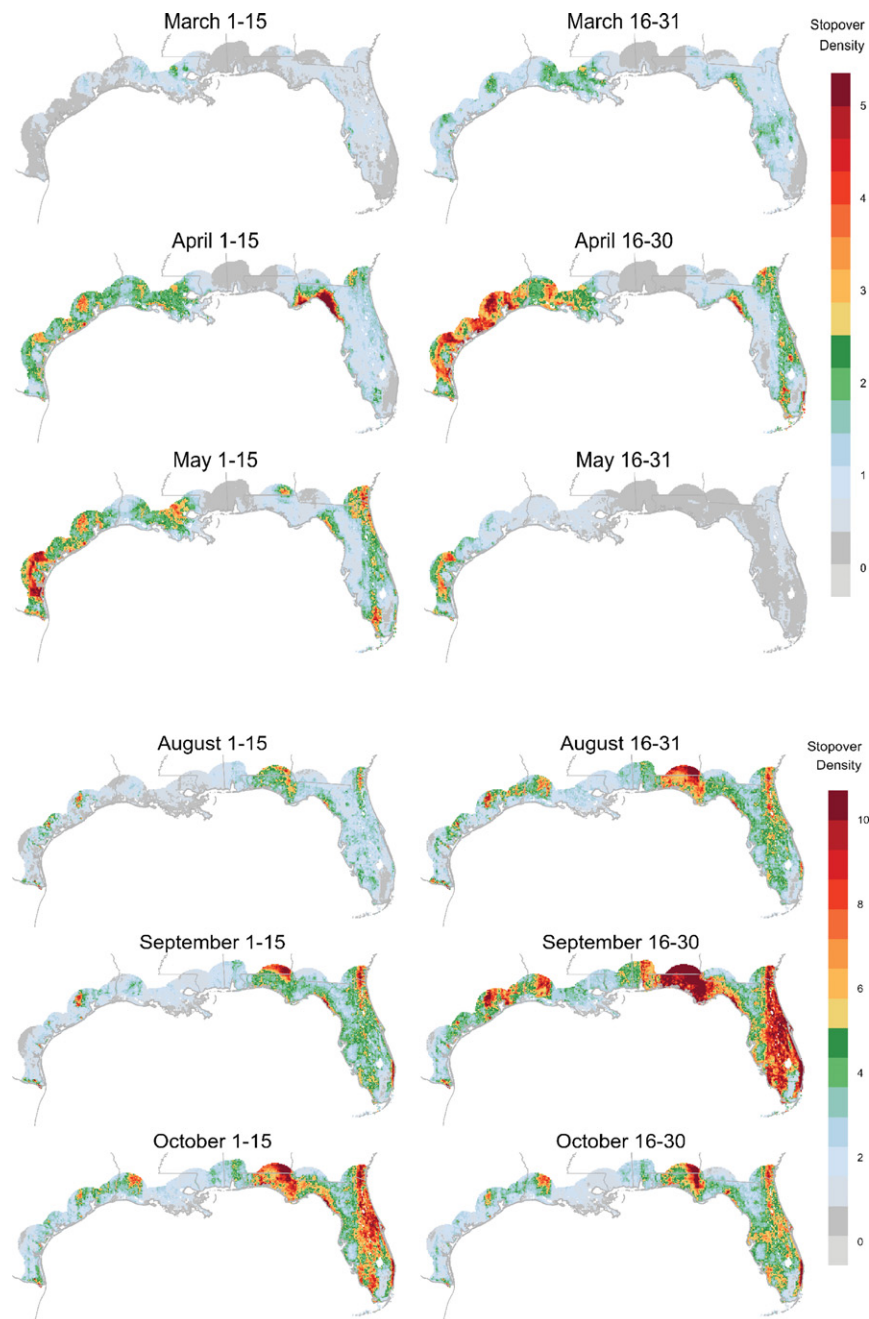
**Figure 4** Mean density of migrating birds departing stopover habitat during spring and autumn migration around the Gulf of Mexico and Atlantic coasts of the south-eastern US classified for each season as low (<50%), moderate (50–85%) and high (>85%) density. The level of daily variability within the high-density category was further categorised as low (<25%), moderate (25–75%) or high (>75%) interpolated from data collected by 12 weather surveillance radars over 8 years (2008–2015). In the bottom panel on stopover consistency across spring and autumn, areas are moderate (green) if they are classified as at least moderate density during both seasons and high (red) if they are classified as high density during both seasons (any daily variability).

Stopover and passage densities followed similar seasonal spatiotemporal patterns; they were considerably higher and shifted eastward in autumn as compared to spring. This pattern corresponds with the higher numbers of migrating birds in autumn as young of the year migrate southward from eastern forests and a wind-driven flyway that shifts birds further west in the spring (Gauthreaux *et al.* 2006; La Sorte *et al.*, 2016; Dokter *et al.*, 2018). In contrast, SPR was negatively related to the spatiotemporal pulse of migration. Temporally, it was higher during the spring season, when the magnitude of migration was lower, and lowest during peak passage times within seasons. Geographically, SPR was higher away from peak seasonal flyways.

Geographical patterns in SPR may be the result of species and population-specific site selection; for example, the high eastern spring values could reflect the routes of birds from South America making first landfall after non-stop flights

(Cano *et al.*, 2020). Migrants from South America can make first landfall as far inland as the Central US and southern Canada, although most stop along the Gulf of Mexico coast (Gómez *et al.*, 2017). The increase in stopover density with distance from the coast during autumn suggests that the relatively lower SPR in autumn may be because more migrants stop in forests further inland, outside of the study area, or land initially on the coast and re-orient further inland to landscapes with greater forest cover that may also have reduced competition for food resources (Sandberg and Moore, 1996; Buler *et al.*, 2007; Smolinsky *et al.*, 2013).

The temporal pattern in SPR of higher ratios during early and late migration could correspond with departure of primarily locally breeding or wintering residents, population or species-specific stopover site selection, or behavioural changes in propensity to stopover as the season progresses (Jenni and Schaub, 2003; Langin *et al.*, 2009; Cohen *et al.*, 2019). For the



**Figure 5** Mean stopover density ( $\text{cm}^2 \text{ha}^{-1}$ ) of migrating birds along the Gulf of Mexico and Atlantic coasts of the south-eastern US during biweekly periods from early to late spring and early to late autumn interpolated from data collected by 12 weather surveillance radars over 8 years (2008–2015).

latter, birds can adjust the frequency of *en route* stops in response to within-season changes in weather patterns, time pressure or food availability to recalibrate the route, energetics or pace of migration (Jenni and Schaub, 2003; Paxton and Moore, 2017). We present the first region-wide maps of within-season geographical variability in stopover density and these spatial and temporal patterns in SPR and stopover density highlight the need for future research. While the magnitude of passage has been estimated across migration systems (Hahn *et al.*, 2009; Dokter *et al.*, 2018; Horton *et al.* 2019), and stopover densities have been mapped for several regions during one

season or another (Ruth *et al.*, 2012; Buler and Dawson, 2014; Lafleur *et al.*, 2016; Archibald *et al.*, 2017), the question of where and when migrating communities stop *en masse* relative to passage rates, and within and between seasons, remains an open question for migration systems globally.

Elucidating the importance of stopover areas for migrating species also requires consideration of context, for example, why birds are stopping at particular sites. Long-distance migrations are sustained by the necessity of places to acquire crucial food to refuel for flights and places to rest between flights or during unfavourable conditions (Gauthreaux 1999;



Moore, , 2018). Our comprehensive modelling of bird stopover distributions across this region supports important seasonal differences in the function of coastal sites. We found birds concentrated near the coastline during spring where they were less influenced by landscape composition, characteristic of fallout to rest (Gauthreaux *et al.* 2006; Lafleur *et al.*, 2016; Clipp *et al.*, 2020), while birds stopped further inland during autumn in landscapes with increased forest cover, characteristic of habitat selection for refuelling (Buler and Moore, 2011). When spring weather conditions are favourable, coastal habitats may offer refuge for birds that are young, physiologically stressed, dehydrated or in poor energetic condition incapable of sustained flight (Spengler *et al.*, 1995; Leberg *et al.*, 1996). Follow-on research could inform targeted habitat management, with finer-resolution measures of SPR incorporating geographical and temporal variability in the characteristics of individuals and passage of species and populations.

Areas where SPR is high and stopover density is low demonstrate that density of use alone is not a comprehensive measure of the conservation value of a stopover site for migrating birds. The negative relationship between the absolute numbers of migrants and the proportion stopping raises important questions about conservation priorities that have not been addressed before. For example, the spring densities of migrants stopping across the panhandle of Florida (KEVX, KTLH) and south Florida (KAMX) are not as high as they are in the western Gulf of Mexico, yet the SPR is very high there. Moreover Florida may be an important flyway, providing needed stopover habitat for trans-Caribbean migrants. Therefore, areas with high SPR may be relatively more important for migrants than those with greater absolute densities. Do we target areas for conservation where the absolute densities support high use over areas where SPR supports high selection by passage migrants, migratory bottlenecks (Bayly *et al.*, 2018)? Maps of between season stopover habitat concentrations across an entire region and areas that are consistently used between seasons may have relatively higher conservation value than those used only during one season or the other. Because we can quantify the proportion of passage migrants that select a stopover site and map stopover habitat use within and between seasons across entire regions, we may need to rethink how we can prioritise stopover areas for conservation (Cohen *et al.*, 2017).

We used the best available data for estimating SPR, but the approach relies on several simplifying assumptions that could introduce biases. Most importantly, we only measured passage flights of nocturnal migrants during the night, while flights across the Gulf of Mexico coast in spring extend into the day (Gauthreaux & Belser 1998), potentially biasing SPR high in spring. Passage is based on net aggregate bird flight density aloft through time; short nocturnal flights by migrants moving locally to relocate to new stopover sites (e.g. Mills *et al.*, 2011) could bias these measures and their implications should be explored in future work as could arrival or departure of migrants that breed or over-winter in these areas. Furthermore, SPR was potentially biasing by differing sampling days among the radars, due to filtering of weather and other clutter, limiting assessment of interannual variability. Lastly, more estimates of departure timing from individual radio-marked birds can improve the accuracy of the cumulative

proportion of birds sampled at exodus from stopover (e.g. Sjöberg *et al.*, 2015). Future fieldwork to ground-truth estimated relative stopover densities as well as species-specific measures of breeding and over-wintering departure and arrival timing and stopover distributions and characteristics of migrants (i.e. age and sex ratios) will advance understanding of the processes by which migrating birds are filtered from air-space into terrestrial habitats.

We predicted stopover habitat use region-wide (i.e. within and outside of areas covered by radar) to identify high-priority landscapes where property acquisition, habitat restoration, air-space reserves and dynamic conservation efforts have the potential to have outsized impacts on migratory bird populations. For example, the Big Bend region of North-Central Florida emerges as an area with consistently high densities of stopover during spring and autumn. This region is one of the largest remaining undeveloped coastlines in continental US and, although migrating birds have not been a primary focus of management efforts, their densities there exemplify how local management and conservation efforts may benefit many species (Walker *et al.*, 2013; Dohner, 2017). Additional high-priority landscapes include Central Texas's Columbia Bottomlands (Rosen *et al.*, 2008) and the Oak-Hackberry forests of Louisiana's Chenier plain (Holcomb *et al.*, 2015), both of which support many species in forests threatened by agricultural, residential and commercial development. Our results can serve as baselines for measurement of effectiveness of future management and conservation efforts on densities of migrating birds. As declines of most migratory bird species outpace current management interventions (Rosenberg *et al.*, 2019), we identify convergence at 'migratory hotspots' where targeted management efforts could uniquely benefit the declining abundance of migratory communities (Cohen and Satterfield, 2020).

## ACKNOWLEDGEMENTS

The authors thank the National Weather Service within the National Oceanic and Atmospheric Administration for access to radar data. Additionally, the authors also thank many undergraduate students from the University of Delaware for help with data processing and analyses. This work was supported by the National Fish and Wildlife Foundation's Gulf Coast Conservation Grants Program 2016–2019, NSF grants 1633206, 1661259 and 1927743, the Edward W. Rose postdoctoral fellowship and the Leon Levy Foundation.

## AUTHORSHIP

EBC, AF, PPM and JJB conceived the study. EBC, HLC, KGH, DS, JAS and JJB compiled and processed radar and covariate data. JJB, KGH and DS developed the data filters; and EBC and JJB performed modelling work. EBC wrote the first draft of the manuscript and all authors contributed substantially to revisions.

## PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ele.13618>.

## DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.mkkwh70xh>.

## REFERENCES

- Åkesson, S. & Hedenström, A. (2000). Wind selectivity of migratory flight departures in birds. *Behav. Ecol. Sociobiol.*, 47, 140–144.
- Alerstam, T. (2003). Bird migration speed. In: *Avian Migration* (eds Berthold, P., Gwinner, E. & Sonnenschein, E.). Springer, Berlin, pp. 253–267.
- Alerstam, T. & Lindström, Å. (1990). Optimal bird migration: The relative importance of time, energy, and safety. In: *Bird Migration* (ed Gwinner, E.). Springer, Berlin, Heidelberg, pp. 331–351.
- Archibald, K.M., Buler, J.J., Smolinsky, J.A. & Smith, R.J. (2017). Migrating birds reorient toward land at dawn over the Great Lakes, USA. *Auk*, 134, 193–201.
- Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *J. Stat. Softw.*, 67, 1–48.
- Bauer, S., Shamoun-Baranes, J., Nilsson, C., Farnsworth, A., Kelly, J.F., Reynolds, D.R. *et al.* (2019). The grand challenges of migration ecology that radar aeroecology can help answer. *Ecography*, 42, 861–875.
- Bayly, N.J., Gómez, C. & Hobson, K.A. (2013). Energy reserves stored by migrating Gray-cheeked Thrushes *Catharus minimus* at a spring stopover site in northern Colombia are sufficient for a long-distance flight to North America. *The Ibis*, 155, 271–283.
- Bayly, N.J., Rosenberg, K.V., Easton, W.E., Gómez, C., Carlisle, J., Ewert, D.N. *et al.* (2018). Major stopover regions and migratory bottlenecks for Nearctic-Neotropical landbirds within the Neotropics: a review. *Bird Conserv. Int.*, 28, 1–26.
- Browning, K.A. & Wexler, R. (1968). The determination of kinematic properties of a wind field using Doppler radar. *J. Appl. Meteorol.*, 7, 105–113.
- Buler, J.J., Barrow, W.C., Boone, M.E., Dawson, D.K., Diehl, R.H., Moore, F.R. *et al.* (2017). Linking animals aloft with the terrestrial landscape. In: *Aeroecology* (eds Chilson, P.B., Frick, W.F., Kelly, J.F. & Liechti, F.). Springer International Publishing, Cham, pp. 347–378.
- Buler, J.J. & Dawson, D.K. (2014). Radar analysis of fall bird migration stopover sites in the northeastern US. *The Condor*, 116, 357–370.
- Buler, J.J. & Diehl, R.H. (2009). Quantifying bird density during migratory stopover using weather surveillance radar. *Geosci. Remote Sens. IEEE Trans. On*, 47, 2741–2751.
- Buler, J.J. & Moore, F.R. (2011). Migrant–habitat relationships during stopover along an ecological barrier: extrinsic constraints and conservation implications. *J. Ornithol.*, 152, 101–112.
- Buler, J.J., Moore, F.R. & Woltmann, S. (2007). A multi-scale examination of stopover habitat use by birds. *Ecology*, 88, 1789–1802.
- Cabrera-Cruz, S.A., Mabee, T.J. & Patraça, R.V. (2013). Using theoretical flight speeds to discriminate birds from insects in radar studies. *The Condor*, 115, 263–272.
- Cabrera-Cruz, S.A., Smolinsky, J.A. & Buler, J.J. (2018). Light pollution is greatest within migration passage areas for nocturnally-migrating birds around the world. *Sci. Rep.*, 8, 3261.
- Cano, N., Bayly, N.J. & Wilson, S. (2020). Is there more than one way to cross the Caribbean Sea? Migratory strategies of Nearctic-Neotropical landbirds departing from northern Colombia. *Journal of Avian Biology*, 51(7), 1–13. <https://doi.org/10.1111/jav.02394>.
- Chernetsov, N. (2006). Habitat selection by nocturnal passerine migrants en route: mechanisms and results. *J. Ornithol.*, 147, 185–191.
- Chilson, P.B., Frick, W.F., Stepanian, P.M., Shipley, J.R., Kunz, T.H. & Kelly, J.F. (2012). Estimating animal densities in the atmosphere using weather radar: To Z or not to Z? *Ecosphere*, 3(8), 1–19.
- Clipp, H.L., Cohen, E.B., Smolinsky, J.A., Horton, K.G., Farnsworth, A. & Buler, J.J. (2020). Broad-scale weather patterns encountered during flight influence Landbird stopover distributions. *Remote Sens.*, 12, 565.
- Cohen, E.B., Barrow, W.C., Buler, J.J., Deppe, J.L., Farnsworth, A., Marra, P.P. *et al.* (2017). How do en route events around the Gulf of Mexico influence migratory landbird populations? ¿Cómo los eventos en ruta alrededor del Golfo de México influyen a las poblaciones de aves terrestres migratorias? Landbird migration and the Gulf of Mexico. *The Condor*, 119, 327–343.
- Cohen, E.B., Pearson, S.M. & Moore, F.R. (2014). Effects of landscape composition and configuration on migrating songbirds: inference from an individual-based model. *Ecol. Appl.*, 24, 169–180.
- Cohen, E.B., Rushing, C.R., Moore, F.R., Hallworth, M.T., Hostetler, J.A., Ramirez, M.G. *et al.* (2019). The strength of migratory connectivity for birds en route to breeding through the Gulf of Mexico. *Ecography*, 42, 658–669.
- Cohen, E.B. & Satterfield, D.A. (2020). ‘Chancing on a spectacle’: co-occurring animal migrations and interspecific interactions. *Ecography*, 43, 1–15. <https://doi.org/10.1111/ecog.04958>.
- De'ath, G. (2007). Boosted trees for ecological modeling and prediction. *Ecology*, 88, 243–251.
- Deppe, J.L., Ward, M.P., Bolus, R.T., Diehl, R.H., Celis-Murillo, A., Zenzal, T.J. *et al.* (2015). Fat, weather, and date affect migratory songbirds' departure decisions, routes, and time it takes to cross the Gulf of Mexico. *Proc. Natl Acad. Sci.*, 112, E6331–E6338.
- Dohner, C. (2017). *Next Steps for a Healthy Gulf of Mexico Watershed*. Fish & Wildlife Service, U.S.
- Dokter, A.M., Desmet, P., Spaaks, J.H., van Hoey, S., Veen, L., Verlinden, L. *et al.* (2019). bioRad: biological analysis and visualization of weather radar data. *Ecography*, 42, 852–860.
- Dokter, A.M., Farnsworth, A., Fink, D., Ruiz-Gutierrez, V., Hochachka, W.M., Sorte, F.A.L. *et al.* (2018). Seasonal abundance and survival of North America's migratory avifauna determined by weather radar. *Nat. Ecol. Evol.*, 2, 1603–1609.
- Elith, J., Leathwick, J.R. & Hastie, T. (2008). Boosted regression trees—a new technique for modelling ecological data. *J. Anim. Ecol.*, 77, 802–813.
- Gauthreaux, S.A. Jr (1999). Neotropical migrants and the Gulf of Mexico: the view from aloft. In: *Gatherings of Angels: migrating Birds and Their Ecology* (ed Able, K.P.). Cornell University Press, Ithaca, NY.
- Gauthreaux, S.A. & Belser, C.G. (1998). Displays of bird movements on the WSR-88D: Patterns and quantification. *Weather Forecast.*, 13, 453–464.
- Gauthreaux, S.A., Belser, C.G. & Welch, C.M. (2006). Atmospheric trajectories and spring bird migration across the Gulf of Mexico. *J. Ornithol.*, 147, 317–325.
- Gómez, C., Bayly, N.J., Norris, D.R., Mackenzie, S.A., Rosenberg, K.V., Taylor, P.D. *et al.* (2017). Fuel loads acquired at a stopover site influence the pace of intercontinental migration in a boreal songbird. *Sci. Rep.*, 7, 1–11.
- Gudmundsson, G.A., Lindström, Å. & Alerstam, T. (1991). Optimal fat loads and long-distance flights by migrating Knots *Calidris canutus*, Sanderlings *C. alba* and Turnstones *Arenaria interpres*. *The Ibis*, 133, 140–152.
- Hahn, S., Bauer, S. & Liechti, F. (2009). The natural link between Europe and Africa – 2.1 billion birds on migration. *Oikos*, 118, 624–626.
- Hedenström, A. (2008). Adaptations to migration in birds: behavioural strategies, morphology and scaling effects. *Philos. Trans. R. Soc. B Biol. Sci.*, 363, 287–299.
- Hedenström, A. & Alerstam, T. (1997). Optimum fuel loads in migratory birds: distinguishing between time and energy minimization. *J. Theor. Biol.*, 189, 227–234.
- Hijmans, R.J., Phillips, S., Elith, J.L. (2017). *dismo: Species Distribution Modeling*. An R package.
- Holcomb, S.R., Bass, A.A., Reid, C.S., Seymour, M.A., Lorenz, N.F., Gregory, B.B. *et al.* (2015). Louisiana State Wildlife Action Plan. Louisiana Wildlife and Fisheries.

- Horn, J.W. & Kunz, T.H. (2008). Analyzing NEXRAD Doppler radar images to assess nightly dispersal patterns and population trends in Brazilian free-tailed bats (*Tadarida brasiliensis*). *Integr. Comp. Biol.*, 48, 24–39.
- Horton, K.G., Sorte, F.A.L., Sheldon, D., Lin, T.-Y., Winner, K., Bernstein, G. et al. (2020). Phenology of nocturnal avian migration has shifted at the continental scale. *Nat. Clim. Change*, 10, 63–68.
- Horton, K.G., Van Doren, B.M., La Sorte, F.A., Cohen, E.B., Clipp, H.L., Buler, J.J. et al. (2019). Holding steady: Little change in intensity or timing of bird migration over the Gulf of Mexico. *Glob. Change Biol.*, 25, 1106–1118.
- Hu, G., Lim, K.S., Horvitz, N., Clark, S.J., Reynolds, D.R., Sapir, N. et al. (2016). Mass seasonal bioflows of high-flying insect migrants. *Science*, 354, 1584–1587.
- Huete, A., Didan, K., van Leeuwen, W., Miura, T. & Glenn, E. (2011). MODIS vegetation indices. In: *Land Remote Sensing and Global Environmental Change: NASA's Earth Observing System and the Science of ASTER and MODIS, Remote Sensing and Digital Image Processing* (eds Ramachandran, B., Justice, C.O. & Abrams, M.J.). Springer, New York, NY, pp. 579–602.
- Jenni, L. & Schaub, M. (2003). Behavioural and physiological reactions to environmental variation in bird migration: a review. In: *Avian Migration* (eds Berthold, P., Gwinner, E. & Sonnenschein, E.). Springer, Berlin, Heidelberg, pp. 155–171.
- Kelly, J.F. & Horton, K.G. (2016). Toward a predictive macrosystems framework for migration ecology. *Glob. Ecol. Biogeogr.*, 25, 1159–1165.
- Kitorov, P., Bairlein, F. & Dubinin, M. (2008). The importance of landscape context for songbirds on migration: body mass gain is related to habitat cover. *Landsc. Ecol.*, 23, 169–179.
- La Sorte, F.A., Fink, D., Hochachka, W.M. & Kelling, S. (2016). Convergence of broad-scale migration strategies in terrestrial birds. *Proc. R. Soc. B Biol. Sci.*, 283, 20152588.
- Laflaur, J.M., Buler, J.J. & Moore, F.R. (2016). Geographic position and landscape composition explain regional patterns of migrating landbird distributions during spring stopover along the northern coast of the Gulf of Mexico. *Landsc. Ecol.*, 31, 1697–1709.
- Langin, K.M., Marra, P.P., Németh, Z., Moore, F.R., Kyser, T.K. & Ratcliffe, L.M. (2009). Breeding latitude and timing of spring migration in songbirds crossing the Gulf of Mexico. *J. Avian Biol.*, 40, 309–316.
- Larkin, R.P. (1991). Flight speeds observed with radar, a correction: slow “birds” are insects. *Behav. Ecol. Sociobiol.*, 29, 221–224.
- Leberg, P.L., Spengler, T.J. & Barrow, W.C. (1996). Lipid and water depletion in migrating passerines following passage over the Gulf of Mexico. *Oecologia*, 106, 1–7.
- Lin, T.-Y., Winner, K., Bernstein, G., Mittal, A., Dokter, A.M., Horton, K.G. et al. (2019). MistNet: Measuring historical bird migration in the US using archived weather radar data and convolutional neural networks. *Methods Ecol. Evol.*, 10, 1908–1922.
- Lindstrom, A. (1990). The role of predation risk in stopover habitat selection in migrating bramblings, *Fringilla montifringilla*. *Behav. Ecol.*, 1, 102–106.
- Loria, D.E. & Moore, F.R. (1990). Energy demands of migration on red-eyed vireos, *Vireo olivaceus*. *Behav. Ecol.*, 1, 24–35.
- McCabe, J.D., Olsen, B.J., Osti, B. & Koons, P.O. (2018). The influence of wind selectivity on migratory behavioral strategies. *Behav. Ecol.*, 29, 160–168.
- McLaren, J.D., Buler, J.J., Schreckengost, T., Smolinsky, J.A., Boone, M., van Loon, E.E. et al. (2018). Artificial light at night confounds broad-scale habitat use by migrating birds. *Ecol. Lett.*, 21, 356–364.
- Mesinger, F., DiMego, G., Kalnay, E., Mitchell, K., Shafran, P.C., Ebisuzaki, W. et al. (2006). North American regional reanalysis. *Bull. Am. Meteorol. Soc.*, 87, 343–360.
- Mills, A.M., Thurber, B.G., Mackenzie, S.A. & Taylor, P.D. (2011). Passerines use Nocturnal Flights for Landscape-Scale Movements during Migration. *The Condor*, 113, 597–607.
- Moore, F.R. (1999). Cheniers of Louisiana and the stopover ecology of migrant landbirds. In: *Gatherings of angels migrating birds and their ecology* (ed Able, K.P.). Cornell University Press, Ithaca, NY, pp. 51–62.
- Moore, F.R. (2018). Biology of landbird migrants: a stopover perspective. *Wilson J. Ornithol.*, 130, 1–12.
- Mouritsen, H. (2018). Long-distance navigation and magnetoreception in migratory animals. *Nature*, 558, 50–59.
- Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. et al. (2008). A movement ecology paradigm for unifying organismal movement research. *Proc. Natl Acad. Sci.*, 105, 19052–19059.
- Nilsson, C., Dokter, A.M., Verlinden, L., Shamoun-Baranes, J., Schmid, B., Desmet, P. et al. (2019). Revealing patterns of nocturnal migration using the European weather radar network. *Ecography*, 42, 876–886.
- NOAA (2012). Version 4 DMSP-OLS Nighttime Lights Time Series. National Geophysical Data Center.
- NOAA (2016). *Coastal Change Analysis Program (C-CAP) Regional Land Cover*. Office for Coastal Management, Charleston, SC.
- Paxton, K.L. & Moore, F.R. (2017). Connecting the dots: Stopover strategies of an intercontinental migratory songbird in the context of the annual cycle. *Ecol. Evol.*, 7, 6716–6728.
- R Core Team (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rosen, D.J., De Steven, D. & Lange, M.L. (2008). Conservation strategies and vegetation characterization in the Columbia Bottomlands, an under-recognized southern floodplain forest formation. *Nat. Areas J.*, 28(4), 74–82.
- Rosenberg, K.V., Dokter, A.M., Blancher, P.J., Sauer, J.R., Smith, A.C., Smith, P.A. et al. (2019). Decline of the North American avifauna. *Science*, 366, 120–124.
- Ruth, J.M., Diehl, R.H. & Felix, R.K. (2012). Migrating Birds' use of stopover habitat in the Southwestern United States. *The Condor*, 114, 698–710.
- Sandberg, R. & Moore, F.R. (1996). Fat stores and arrival on the breeding grounds: reproductive consequences for passerine migrants. *Oikos*, 77, 577–581.
- Schaub, M., Liechti, F. & Jenni, L. (2004). Departure of migrating European robins, *Erithacus rubecula*, from a stopover site in relation to wind and rain. *Anim. Behav.*, 67, 229–237.
- Shamoun-Baranes, J., Alves, J.A., Bauer, S., Dokter, A.M., Hüppop, O., Koistinen, J. et al. (2014). Continental-scale radar monitoring of the aerial movements of animals. *Mov. Ecol.*, 2, 9.
- Shamoun-Baranes, J., Liechti, F. & Vansteelant, W.M.G. (2017). Atmospheric conditions create freeways, detours and tailbacks for migrating birds. *J. Comp. Physiol. A*, 203, 509–529.
- Sheldon, D. (2015). WSRLIB: MATLAB toolbox for weather surveillance radar.
- Sheldon, D., Farnsworth, A., Irvine, J., Van Doren, B., Webb, K., Dietterich, T.G. et al. (2013). Approximate Bayesian inference for reconstructing velocities of migrating birds from weather radar. AAAI Conference on Artificial Intelligence, North America, June 2013. Available at: <http://www.aaai.org/ocs/index.php/AAAI/AAAI13/paper/view/6468>. Last accessed 28 July 2020.
- Sjöberg, S., Alerstam, T., Åkesson, S., Schulz, A., Weidauer, A., Coppack, T. et al. (2015). Weather and fuel reserves determine departure and flight decisions in passerines migrating across the Baltic Sea. *Anim. Behav.*, 104, 59–68.
- Smolinsky, J.A., Diehl, R.H., Radzio, T.A., Delaney, D.K. & Moore, F.R. (2013). Factors influencing the movement biology of migrant songbirds confronted with an ecological barrier. *Behav. Ecol. Sociobiol.*, 67, 2041–2051.
- Spengler, T.J., Leberg, P.L. & Barrow, W.C. (1995). Comparison of Condition Indices in Migratory Passerines at a Stopover Site in Coastal Louisiana. *The Condor*, 97, 438–444.
- Stepanian, P.M. & Wainwright, C.E. (2018). Ongoing changes in migration phenology and winter residency at Bracken Bat Cave. *Glob. Change Biol.*, 24, 3266–3275.

- Van Doren, B.M. & Horton, K.G. (2018). A continental system for forecasting bird migration. *Science*, 361, 1115–1118.
- Van Doren, B.M., Horton, K.G., Dokter, A.M., Klinck, H., Elbin, S.B. & Farnsworth, A. (2017). High-intensity urban light installation dramatically alters nocturnal bird migration. *Proc. Natl Acad. Sci.*, 114, 11175–11180.
- Walker, L., Pease, C., DeVore, D., Woodrow, W., Clevensine, R. & Riley, C. (2013). *Vision for a Healthy Gulf of Mexico Watershed*. Fish & Wildlife Service, U.S.

Editor, Tim Coulson

Manuscript received 30 July 2020

First decision made 24 August 2020

Manuscript accepted 9 September 2020

#### SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.