

**Title:** Holding steady: little change in intensity or timing of bird migration over the Gulf of Mexico

**Running head:** Bird migration over the Gulf of Mexico

**Authors:** Kyle G. Horton<sup>1\*</sup>, Benjamin M. Van Doren<sup>2</sup>, Frank A. La Sorte<sup>1</sup>, Emily B. Cohen<sup>3</sup>, Hannah Clipp<sup>4</sup>, Jeffrey J. Buler<sup>4</sup>, Daniel Fink<sup>1</sup>, Jeffrey F. Kelly<sup>5,6</sup>, and Andrew Farnsworth<sup>1</sup>

**Affiliations:**

<sup>1</sup>Cornell Lab of Ornithology, Cornell University, Ithaca, NY, USA.

<sup>2</sup>Edward Grey Institute, Department of Zoology, University of Oxford, Oxford, OX1 3PS, UK

<sup>3</sup>Migratory Bird Center, Smithsonian Conservation Biology Institute, National Zoological Park, Washington, DC, USA

<sup>4</sup>Department of Entomology and Wildlife Ecology, University of Delaware, Newark, DE, USA.

<sup>5</sup>Department of Biology, University of Oklahoma, Norman, OK, USA.

<sup>6</sup>Corix Plains Institute, University of Oklahoma, Norman, OK, USA.

**\*Corresponding author:** Kyle G. Horton, Cornell Lab of Ornithology, Cornell University, 159 Sapsucker Woods Rd., Ithaca, New York, USA. Phone: (716) 279- 5710. Email: kgh48@cornell.edu

**Keywords:** climate change, eBird, Gulf of Mexico, migratory birds, phenology, weather surveillance radar

**Paper type:** Research Article

**Abstract:**

Quantifying the timing and intensity of migratory movements is imperative for understanding impacts of changing landscapes and climates on migratory bird populations. Billions of birds migrate in the Western Hemisphere, but accurately estimating the population size of one migratory species, let alone hundreds, presents numerous obstacles. Here, we quantify the timing, intensity, and distribution of bird migration through one of the largest migration corridors in the Western Hemisphere, the Gulf of Mexico (the Gulf). We further assess if there have been changes in migration timing or intensity through the Gulf. To achieve this, we integrate citizen science (eBird) observations with 21 years of weather surveillance radar data (1995-2015). We predicted no change in migration timing and a decline in migration intensity across the time series. We estimate that an average of 2.1 billion birds pass through this region each spring en route to Nearctic breeding grounds. Annually, half of these individuals pass through the region in just 18 days, between April 19<sup>th</sup> and May 7<sup>th</sup>. The western region of the Gulf showed a mean rate of passage 5.4 times higher than the central and eastern regions. We did not detect an overall change in the annual numbers of migrants (2007-2015) or the annual timing of peak migration (1995-2015). However, we found that the earliest seasonal movements through the region occurred significantly earlier over time (1.6 days decade<sup>-1</sup>). Additionally, body mass and migration distance explained the magnitude of phenological changes, with the most rapid advances occurring with an assemblage of larger-bodied shorter-distance migrants. Our results provide baseline information that can be used to advance our understanding of the developing implications of climate change, urbanization, and energy development for migratory bird populations in North America.

## **Introduction:**

Avian migration is a global phenomenon with movements spanning thousands of kilometers through diverse environments (Newton, 2003), but quantifying first-principle parameters of migration, such as volume and timing, to characterize this phenomenon at large spatial extents has proven challenging. These measures are critical for quantifying animal movement responses to changing landscapes and climates (Kelly & Horton, 2016). With mounting evidence of phenological shifts and population declines there is an immediate need for testing hypotheses within and among migratory systems (Both, Bouwhuis, Lessells, & Visser, 2006; Cohen, Lajeunesse, & Rohr, 2018; Parmesan & Yohe, 2003; Thackeray et al., 2016; Visser, Perdeck, Balen, & Both, 2009; Walther et al., 2002).

Estimates of the numbers of individual birds involved in nocturnal migration – the primary diel period of movement for most terrestrial species – range in the millions (Gauthreaux, 1971; Horton, Van Doren, Stepanian, Hochachka, et al., 2016; Van Doren & Horton, 2018) and may approach the billions when accounting for full season movements across broad geographic regions (Dokter et al., 2018; Hahn, Bauer, & Liechti, 2009). However, objective estimates of the number of individuals that undertake nocturnal migration within North America are largely unavailable (Rich et al., 2004). The importance of estimating the passage of migrants cannot be overemphasized, with a large body of literature highlighting recent declines in migratory bird populations (Askins, Lynch, & Greenberg, 1990; Both et al., 2006; Gauthreaux, 1992; Møller, Rubolini, & Lehikoinen, 2008; Nebel, Mills, McCracken, & Taylor, 2010; Robbins, Sauer, Greenberg, & Droege, 1989). Natural and anthropogenic obstacles abound for migrating birds, including predation (Cimprich & Moore, 1999; Loss, Will, & Marra, 2013b), habitat degradation

and destruction (Norris & Marra, 2007; Norris, Marra, Kyser, Sherry, & Ratcliffe, 2004), collisions with structures (e.g., buildings, communication towers, wind turbines) (Loss, Will, Loss, & Marra, 2014; Loss, Will, & Marra, 2013a), and attraction to artificial light at night (Cabrera-Cruz, Smolinsky, & Buler, 2018; La Sorte, Fink, Buler, Farnsworth, & Cabrera-Cruz, 2017; McLaren et al., 2018; Van Doren et al., 2017). In addition to these factors, another fundamental challenge for migratory birds is shifts in resource availability induced by global climate change (IPCC 2013), which has the potential to affect all aspects of their annual life cycle, including migration (Møller, Fiedler, & Berthold, 2010).

Within North America the northern coast of the Gulf of Mexico (hereafter the Gulf) is an ecologically important region for the passage of spring migrants. Migrants leaving the Caribbean and Central and South America cross the Gulf (trans-Gulf) or travel around the Gulf (circum-Gulf) (Gauthreaux & Belser, 1999; Lowery, 1946; Stevenson, 1957). These coastal regions are vital for birds to make successful journeys, as they provide the first possible terrestrial stopover locations following overwater flights, allowing birds to replenish depleted fat stores and take shelter in adverse conditions (Moore, 2018). With the vast majority of long-distance migrants (i.e., migrants wintering south of the Gulf of Mexico) passing through this geographic region, quantifying where and when migrants move over and around the Gulf is fundamental for understanding how these patterns may be changing, particularly important given increased anthropogenic threats, including habitat and climate change, with which migrant populations must contend.

Migratory birds may be particularly vulnerable to climate change in the geographically disparate areas they use throughout their annual cycle (Bairlein & Winkel, 2001). For example, decreasing rainfall, and consequently diminished food abundance and body condition, at tropical wintering areas can delay the timing of departure for spring migration (Cooper, Sherry, & Marra, 2015; Gordo, 2007; Saino et al., 2007; Studds & Marra, 2011). Furthermore, phenologies of resources in temperate breeding areas are advancing, many species are arriving earlier (Cohen et al., 2018; Usui, Butchart, & Phillimore, 2017), and behavioral changes may be insufficient to match changes in resources (Mayor et al., 2017); moreover, there may be fitness consequences associated with arrival timing (e.g., Smith & Moore 2005; Møller *et al.* 2009; Gienapp & Bregnballe 2012). Therefore, it is possible that Nearctic-Neotropical migrants are under pressure to increase rates of spring migration. Evidence shows that these migrants can adjust their speeds of migration within eastern North America as they encounter warmer spring temperatures (Marra, Francis, Mulvihill, & Moore, 2005). One long-term analysis of spring phenology at a single location along the Gulf of Mexico found annual variability but no advancement of passage timing, while some species have delayed passage by a few days over the 20-year period (1993-2012; Cohen *et al.* 2015). Cohen *et al.* (2015) also found annual tropical resource phenology was a poor indicator of temperate resource phenology, suggesting that migrants may adjust the rate of migration after crossing the Gulf of Mexico into continental North America. However, this study was done at a single location and no study has comprehensively measured the timing of migration across this critical passage region.

Variation in the arrival time of avian migrants has served as a useful framework for understanding how natural systems are responding to climate change (Both & Visser, 2001;

Hüppop & Winkel, 2006; Hurlbert & Liang, 2012; Jonzén et al., 2006; Marra et al., 2005; Strode, 2003), but the number of large-scale examinations of phenological change in migratory birds is limited. Using data from the broad-scale citizen science project eBird (Sullivan et al., 2014), the quantifications of system-wide phenological change, asynchrony in primary production, and migrant arrival are becoming clearer (Hurlbert & Liang, 2012; Mayor et al., 2017). However, much variation exists geographically and across species. With such variation, it is difficult to make general conclusions across species without standardized abundance measures. Weather surveillance radars (WSR) offer an opportunity to address this problem, as it is a standardized tool for quantifying the abundance of aerial migrants (Kelly & Horton, 2016). Furthermore, although radar data have limited utility for representing species identities, we can build an index of system-based phenology by integrating eBird and WSR data. The integration of these datasets is revealing new insights into macro-scale movements (Horton et al., 2018; Kelly et al., 2016; La Sorte, Hochachka, Farnsworth, Sheldon, Fink, et al., 2015; La Sorte, Hochachka, Farnsworth, Sheldon, Van Doren, et al., 2015) and can add taxonomic resolution to the rich archive of WSR data. To date, such efforts have been primarily proofs-of-concept that this approach can capture properties of complex assemblages of biotic and abiotic factors that characterize multi-dimensional systems, heralding a new paradigm that combines data-intensive science and ecology (Hochachka et al., 2012; Kelling et al., 2009).

Here, we integrate data from eBird and weather surveillance radars to quantify the (1) timing, (2) intensity, (3) distribution and (4) trends in migration timing and intensity of birds passing through the primary migratory corridor in the Western Hemisphere, the Gulf of Mexico. We predict declines in migration intensity through the Gulf of Mexico (Askins et al., 1990; Both et

al., 2006; Robbins et al., 1989) and no change in the timing of migratory movements across the time series of years analyzed (Cohen et al., 2015).

## **Materials and methods:**

### **Weather surveillance radar**

#### *Data processing*

We used unfiltered (i.e., level-II) weather surveillance radar data from 11 stations surrounding the Gulf (Fig. 1), acquired from NOAA's National Centers for Environmental Information, for the period March 1<sup>st</sup> to May 31<sup>st</sup> for each year from 1995-2015. We retained data between evening and morning civil twilight (i.e., when the sun angle was at least 6° below the horizon) and discarded any aerial samples containing precipitation that could obscure bird movements. We only used nights if at least half of the nocturnal period yielded clear samples for biological interpretation. For the characterization of movements, we categorized WSR stations into three regions: western (KCRP, KBRO, KHGX), central (KLCH, KLIX, KMOB, KEVX), and eastern (KTLH, KTBW, KBYX, KAMX).

We determined migrant flight direction (i.e. track) and groundspeed from radial velocity following Browning & Wexler (1968) and migration traffic from reflectivity from 0 to 3000 m above ground level (a.g.l.), at 100 m altitudinal bins, following Farnsworth *et al.* (2016) and Horton *et al.* (2016b). We constructed height profiles of migrant track and intensity from the lowest elevation sweeps (0.5-4.5°) from 5 to 37.5 km. Elevation sweeps are completed every 5 to 10 minutes, and the assemblage of sweeps represents a volume scan, the sampling unit of our processing. When necessary, we dealiased radial velocity measures following Sheldon et al.

(2013) through the WSRLIB package (Sheldon, 2015). To limit insect contamination, we excluded altitudinal bins with velocity azimuth displays with RMSE (root mean squared error) less than one, and we removed samples with RMSE greater than five to limit poor fits (Dokter et al., 2011; Horton, Van Doren, Stepanian, Farnsworth, & Kelly, 2016a). We used samples with northward tracks only ( $< 90^\circ$  and  $> 270^\circ$ , Fig. S1), resulting in an elimination of 14.1% of the data that remained after filtering protocols.

#### *Stationary clutter mitigation*

Prior to the construction of height profiles of activity, we constructed masks to remove stationary clutter from the lowest elevational sweep for each radar for each year. We summed 500 (if available) low elevation scans ( $0.5^\circ$ ), starting on March 1<sup>st</sup> (00:00 UTC) and selected every 5<sup>th</sup> scan (day and night). We classified any pixel above the 85<sup>th</sup> percentile of the summed reflectivity as clutter and masked it from our analysis. As an additional precaution, we replaced the 0-m height bin with the 100-m height bin to reduce clutter contamination but still approximate the complete coverage to the ground.

#### *Data selection*

To discriminate unsuitable volume scans for analysis (e.g., contaminated with precipitation or ground clutter from anomalous beam propagation) from suitable scans (i.e., empty airspace or biologically dominated reflectivity), we designed a random forest classifier using package “randomForest” (Liaw & Wiener, 2002). We trained the classifier on 22,172 manually classified nocturnal volume scans (e.g., Fig. S2), independently classified by KGH and BVD. We used samples with common classification agreement in the training set (93.7 % of scans). We



randomly selected scans for the training set in sequence sets for each radar for each year (mean samples per radar 102 year<sup>-1</sup>). We extracted derived predictor variables from profiles of reflectivity, groundspeed, and summaries of the number of sampling volumes above 35 dBZ (see Table S1 for predictor descriptors). We generated 1000 trees and restricted terminal node size to 50 scans to limit overfitting. The model resulted in 2.64% classification error (see Table S2). As an additional step to reduce the inclusion of false positives (i.e., unsuitable samples classified as suitable), we only used scans with a probability of being uncontaminated of 75% or higher. We processed 1,481,063 nocturnal scans from 1995 to 2015, and 1,161,029 were classified as suitable.

#### *Insect mitigation*

To limit insect contamination, we eliminated data from height bins with airspeeds less than 5 m s<sup>-1</sup> (Gauthreaux & Belser, 1998; Larkin, 1991; Van Doren & Horton, 2018). We calculated airspeeds through vector subtraction using measures of migrant groundspeed, wind direction, and wind speed. We quantified wind direction aloft using the North American Regional Reanalysis (NARR) data set (Mesinger et al., 2006). NARR models zonal and meridional wind components every three hours at 25 hPa increments at a gridded 32-km spatial resolution. We aligned the nearest radar measures by time and height above ground level.

#### **eBird**

To build a species-based perspective of migratory communities moving through the Gulf region, we used spatio-temporal exploratory models (STEM) (Fink et al., 2010) to estimate weekly

probabilities of occurrence of nocturnally migrating bird species using bird observations from eBird (Sullivan et al. 2014) compiled during the period 2004 to 2011. From 446 species with reliable occurrence maps, we classified 143 as nocturnal migrants having probabilities of occurrence greater than 0 in our sampling area (see Table S3). STEM models use underlying landscape (landcover, elevation), temporal (year, day of year, time of day), and effort (duration, distance, number of observers) information to produce probabilities of species occurrence. For the STEM analysis, eBird data were limited to stationary and traveling counts ( $\leq 8.1$  km) with local start times between 05:00 and 20:00 and counts that were less than 3 hours in duration. We rendered weekly estimates of probability of occurrence for each species at 130,751 points at a density of *ca.* 15 per  $30 \times 30$  km within the contiguous USA using a geographically stratified random design (SRD). We used previously described methods to remove SRD points that contained very low probabilities of occurrence (La Sorte et al., 2014). Specifically, we converted weekly estimates of probability of occurrence to zero that were less than or equal to the 80<sup>th</sup> percentile of the non-zero occurrence probabilities for that week, and if the 80<sup>th</sup> percentile was  $<0.0175$ , which defined our minimum probability threshold, the probability threshold was set to 0.0175.

## **Migrant distance**

To estimate migrant distance, we used NatureServe breeding and non-breeding range maps for 143 species (Ridgely et al., 2007). We first converted breeding and wintering range map polygons to collections of equal-area hexagons (cell size of  $12\,452\text{ km}^2$ , Sahr, 2011; Sahr et al., 2003). Following this step, total migration distance was calculated as the great circle (orthodromic) distance between the geographic centroids of the breeding and non-breeding

ranges for each species. Geographic centroids were estimated by averaging the geographic locations of the hexagon cell-centers occurring within each species' breeding and non-breeding ranges (La Sorte, Hochachka, Farnsworth, Dhondt, & Sheldon, 2016). We weighted distances by the probability of occurrence of each species to emphasize distance measures of migrants moving through the radar sampling area.

### **Estimating the number of migrants**

To estimate the number of migrants passing, we first converted reflectivity factor (dBZ) to reflectivity (dB $\eta$ ) following:  $\eta[\text{dB}] = Z[\text{dBZ}] + \beta$ , where  $\beta = 10\log_{10}(10^3\pi^5|K_m|^2/\lambda^4)$  (Chilson et al., 2012). We used an average WSR-88D wavelength ( $\lambda$ ) of 10.7 cm and  $|K_m|^2$  for liquid water of 0.93, the dielectric constant. This yielded  $\beta = 13.37$ . Converting reflectivity factor (Z) to reflectivity ( $\eta$ ) resulted in units of  $\text{cm}^2 \text{ km}^{-3}$ . We converted reflectivity ( $\eta$ ) to birds  $\text{km}^{-3}$  by dividing by the radar cross-sectional (RCS) area of an average-sized migrant passing through the region, as indicated by ground-based observations (see below for RCS quantification).

To account for the flow of migrants over the sampling area and to limit the potential for double counting of migrants between radars, we multiplied birds  $\text{km}^{-3}$  by the northward component of the measured groundspeed ( $\text{km h}^{-1}$ ) and integrated through the night to account for the nightly passage using linear interpolation for area under the curve, resulting in birds  $\text{km}^{-2}$ . We multiplied by the altitudinal resolution (0.1 km) of each altitudinal bin, resulting in birds  $\text{km}^{-1}$ .

Empirically measured radar cross-sections, a measure needed to convert radar reflectivity to number of birds, are difficult to acquire and the number of unique species measured are limited. For this reason, we used previously measured S-band (~10 cm wavelength) radar cross-sections of known species to relate migrant body size (grams) to RCS (Table S4) (Eastwood, 1967; Houghton, Blackwell, Ogilvie, & Wilmot, 1975). Whereas radar theory predicts a complex, non-linear relationship between RCS and reflector size (Stepanian, Horton, Melnikov, Zrnić, & Gauthreaux, 2016), especially of large scatters, like birds, we believe the number of species and variation in aspect relative to the radar will generalize effects of resonance to a broadly linear relationship. We found that body mass explained 89.9% of the variance in RCS measures ( $\log_{10}(\text{cross-section}) = 0.670 (\log_{10}(\text{body mass}))$ ,  $p < 0.001$ , d.f. = 10, Fig. 2a). Using this relationship, we converted the average mass of each species likely to pass through the region to a species-specific RCS (Fig. 2b, Table S3).

We weighted our calculations of mean RCS by the probability of occurrence of each species to emphasize RCS measures of migrants moving through the radar sampling area. We calculated weekly mean probability of occurrence for each species from eBird at each WSR station using the SRD points that occurred within the biological range (80-km radius) of each WSR station. Our weights were the absolute value of the derivative of occurrence, to capture actively migrating species whose rates of detection in an area were therefore either increasing or decreasing. We used a square-root transformation on the occurrence values to reduce the skewness of the distribution, but not completely remove it, as in a log-transformation (Horton et al., 2018). We log-transformed species RCS values before averaging to reduce bias from large-bodied species. We used the weekly estimate of RCS to predict nightly RCS by fitting a

generalized additive model to ordinal date for each WSR station. To determine the sensitivity of our estimates of migrant passage to our calculation of RCS, we made estimates using fixed RCS values and a range of transformations on RCS and species probability of occurrence (Table S5). Because KBYX is located on Key West and samples migrating birds primarily over marine environments where STEM estimates do not exist, we used the next closest radar installation (KAMX) to retain KBYX in our analysis. KBYX and KAMX are separated by roughly 210 km.

Lastly, to measure the total number of birds passing through the region, we used a transect, or turnstile line, spanning the entire Gulf region (1,954 km, Fig. 1). We determined individual radar segments by measuring the distance between the mid-points of the radar locations. Multiplying the northward component of bird traffic at each station (birds km<sup>-1</sup>) by the segment length resulted in the northward component of traffic estimates (i.e., number of birds) for each segment. To encompass the full scope of the movements, we extended the turnstile line beyond the western- and easternmost locations, using 1.75° and 1.25° length segments, respectively. As an additional precaution, we excluded KBRO and KBYX from our estimate of total passage to limit true double counting of migrants (i.e. the same migrant counted on two different radars). We removed these radars because they are positioned at comparable longitudes and proximity of more northerly radars. We must note that we use nocturnal measures only, likely resulting in a more conservative estimate of passage, as some nocturnal migrants may pass our stations during diurnal periods.

## **Migration traffic and phenology analyses**

We examined two primary signals annually, migration intensity (i.e., number of migrants and traffic rate) and migration timing (i.e., the dates at which 5, 25, 50, 75, and 95% of migrants passed).

We determined the average overall number of migrants passing through the entire region by fitting separate generalized additive mixed-models (GAMM) to the data from each radar station, specifying ordinal date as a smooth term and year as a random effect. We used the “quasipoisson” distribution family with log link function to restrict predictions to positive values and generated discrete predictions for each day for each radar, summing all nights to total number of migrants passing the entire region. To determine the magnitude of annual change in migration traffic, we constructed yearly models for each WSR station, fitting a generalized additive model (GAM) to each radar for each year, fitting a spline to ordinal date. We made nightly predictions and summed estimates to calculate the cumulative migration traffic rate (birds  $\text{km}^{-1}$ ). We regressed cumulative migration traffic rate on year. We examined annual change at three levels: the entire Gulf, regional (western, central, and eastern), and individual WSR station.

Because precipitation contamination occluded our ability to make viable traffic estimates on some nights, our dataset contained gaps in the time-series, to which we filled with GAM predictions. These gaps have the potential to bias our traffic estimate if migrant activity correlates with precipitation contamination (e.g., if proportionally fewer birds migrate in the presence of precipitation). To quantify how this distribution of missing data could influence our passage estimates, we randomly subsampled our dataset to demonstrate two extremes: (1) nights with precipitation more likely to have low bird densities and (2) nights with precipitation more

likely to have high bird densities. Additionally, we examined our assumption that nights excluded due to precipitation show the same distribution of bird densities as clear nights. We employed these three sampling strategies by weighting the random selection by the inverse of the square root of the number of birds, square root of the number of birds, and an unweighted random selection.

To determine if migration phenology changed from 1995 to 2015, we calculated the date of peak migration, defined as the date at which half the number of migrants had passed through the region. Additionally, we examined the dates when 5, 25, 75, and 95% of migrants passed. We fit a generalized additive model (GAM) for each year for each radar and calculated the 5, 25, 50, 75, and 95% passage dates from model predictions. Because seasonal radar samples were at times sparse (See Fig. S2), especially in the early years of the radar archive, we only used radars in years when at least five nights in March, April, and May and at least one third of the possible nights (total 92 nights) were sampled (~30 nights). Changes in phenology were calculated by regressing dates of cumulative activity (5, 25, 50, 75, and 95%) on year. To examine if body size and migrant distance were predictive of the rate of phenological change, we regressed mass, distance, and the interaction of mass and distance on phenological change using a linear mixed-effects model with WSR station as a random effect. We calculated 95% confidence intervals from 1000 bootstrapped samples.

In the history of the NEXRAD network, NOAA has implemented a series of upgrades. One subtle, but important, change occurred from November 2005 to September 2006, altering how stationary clutter (e.g., buildings, trees) and potentially low speed targets, like birds, were filtered

(Gaussian Model Adaptive Processing, Chrisman & Ray 2005). Therefore, out of caution, we use data from 2007 to 2015 (9 years) for trend analysis of intensity. We use the full time-series (1995 to 2015) to make phenological estimates, because they are insensitive to these changes.

## **Results:**

The three most commonly occurring orders that passed through the Gulf region were Anseriformes, Charadriiformes, and Passeriformes, and occurrence varied noticeably by geographic location and more subtly over the season (Fig. 3a). Through the season, we observed a higher occurrence of passerines in the central and eastern regions, with the western region showing a higher occurrence of Anseriformes and Charadriiformes. For these reasons, we observed higher body masses for birds moving over the western region. Translating body mass to average radar cross-section, we observed a seasonal range between  $7.6 \text{ cm}^2$  (18.1 g) and  $19.5 \text{ cm}^2$  (69.8 g) at individual stations, with the mean across the regions being  $12.8 \pm 2.1 \text{ cm}^2$  SD (38.1 g),  $10.3 \pm 1.6 \text{ cm}^2$  SD (27.9 g), and  $9.2 \pm 1.2 \text{ cm}^2$  SD (24.0 g) for western, central, and eastern respectively (Fig. 3b). Assemblage migratory distance generally increased through the season and was highest in the western region (Fig. 3c).

Integrating species observations with radar measures, we estimated an average of  $2.1 \pm 0.2$  (SE) billion migrants pass through the Gulf region during spring migration (range 1.7 to 2.6, Fig. 4a, Fig. S4). Our quantification of migrant passage assumed that nights excluded due to precipitation show the same distribution of bird densities as clear nights. Even with strong violations of this assumption, our estimation of traffic only changed by as much as 8.0% (mean  $4.7 \pm 2.4\%$  SD), lending support for our methodology (Fig. S5). Migration traffic was greatest over the western



Gulf. Migration was particularly intense over south and central coast of Texas, and generally diminished moving eastward across the Gulf region (Fig. 4b). The western region had an average migration rate of 26,224 bird km<sup>-1</sup>night<sup>-1</sup>, 5.4 times higher than the central and eastern regions (Fig. 4b). Half of the migrants passing the Gulf region passed in an 18-day period between April 19<sup>th</sup> and May 7<sup>th</sup> (Fig. 4a). Site-specific patterns of phenology were similar across the region, with peaks in late April and early May (Fig. 4b). However, we generally observed earlier and more variable peak dates moving eastward across the Gulf region (Fig. 4c-e).

We did not find a significant change in migration traffic through the entire Gulf from 2007 to 2015 ( $p=0.379$ ). We did find variation across sites and regions (Fig. 5a), with no change detected in the western and central regions ( $p=0.286$  and  $p=0.799$ , respectively) and a significant decline in the eastern region ( $-2.5\pm1.2\%$  year<sup>-1</sup> SE,  $p=0.033$ ).

From 1995 to 2015, we observed a significant advancement ( $1.6\pm0.7$  days decade<sup>-1</sup> SE,  $p=0.035$ ) in the timing of early-season migratory movements (i.e., 5% of cumulative movement, Fig. S6), however we did not see significant changes for later periods (25<sup>th</sup>,  $p=0.518$ ; 50<sup>th</sup>,  $p=0.588$ ; 75<sup>th</sup>,  $p=0.599$ , 95<sup>th</sup>,  $p=0.638$ , Fig. S6). Body mass ( $p=0.005$ ) and migrant distance ( $p=0.020$ ) and the interaction of mass and distance ( $p=0.006$ ) explained the magnitude of phenological change moving through each quantile period, with the most rapid advances occurring with an assemblage of larger-bodied birds and longer-distance migrants (Fig. 5b). Moreover, the change in timing of peak migration exhibited a longitudinal trend across individual radars from earlier in the west to later in the east ( $p=0.015$ , Fig. S6).

## Discussion:

In a unique long-term and large-scale radar dataset, we found that between 1.7 and 2.6 billion nocturnal migrants (mean of  $2.1 \pm 0.2$  SE) pass over the north coast of the Gulf of Mexico during spring migration. Half of these birds pass this important region within an 18-day window, from April 19<sup>th</sup> and May 7<sup>th</sup>, and our findings indicate that neither the overall numbers of birds (2007-2015) nor their peak timing (1995-2015) has changed; however, the earliest seasonal movements (i.e., 5% of cumulative movement) advanced earlier over the duration of our study. Additionally, our findings show that migrants are not distributed evenly along the Gulf coast during spring migration, with the western Gulf used by more migrants than the eastern Gulf (Gauthreaux & Belser, 1999). The results of this study rely heavily on the integration of our two complementary datasets, radar and eBird, to estimate over broad spatial and temporal scales the number and timing of migrants moving into North America. This integration leaves no doubt that the Gulf of Mexico is a critical region for North American migratory bird populations and the changes that occur within this region -- from urbanization to wind energy development -- have the potential to significantly affect many migratory bird populations.

Peak spring migration passage timing was concentrated and consistent among the 21 years considered in this study. This study included long-distance migrant species that spend the winter in the Neotropics and short-distance migrant species that winter locally around the Gulf (See Table S3). While short-distance migrants may be more flexible (Calvert, Mackenzie, Flemming, Taylor, & Walde, 2012; La Sorte et al., 2016), long-distance migrants are under strong endogenous control for departure timing (Berthold, 1996). Within these areas there is no evidence for advancing phenological changes in greenness (Cohen et al., 2015), therefore, it is

not entirely surprising to see relatively consistent median passage timing when departing, crossing, and navigating around the Gulf. Similarly, long-term species-specific comparisons within this region have not found evidence of earlier passage linked with changes in en route spring greening of vegetation (NDVI) for passerines that overwinter in South America (Cohen et al., 2015). In contrast, passerines that overwinter in the Caribbean and Central America have delayed their peak passage by 2 to 3 days over the last 20 years, which has been linked to drier conditions on their wintering areas (Cohen et al., 2015). Consistent with this, the change in median passage at individual radar stations showed a trend of later passage in the eastern Gulf, a region dominated by smaller-bodied passerine species. However, long-distance migrants are adjusting their migration timing to arrive earlier to their breeding grounds (Usui et al., 2017), suggesting this change is occurring after they circumnavigate or cross the Gulf (Marra et al., 2005). We predict the magnitude of phenological change increases with increasing latitude across North America during spring movements. Yet, while adjustments to stopover duration can be made, the growing divide between resource availability and migration initiation may stretch the limit of this phenotypic plasticity (Schmaljohann & Both, 2017), resulting in insufficient adjustments and possibly trophic mismatches (Strode, 2015; Wood & Pidgeon, 2015). Numerous studies of plot-level phenology demonstrate that variation in phenology of individual plant species is impactful for migrant phenology (Strode, 2009; Wood, Pidgeon, Liu, & Mladenoff, 2012). Further effort to scale-up species-level phenology from standardized plot-level measurements is needed.

Our examination of the earliest seasonal movements of migration (i.e., 5% of cumulative movement) revealed earlier passage timing of first migrants at a rate of 1.6 days decade<sup>-1</sup> earlier.

This supports other evidence of earlier migratory movements with a warming climate (Cohen et al., 2018) and likely explained by shifts in the departure of short-distance migrants that overwinter along the northern Gulf, rather than for intercontinental long-distance migrants, since peak passage timing has not consistently shifted. We predicted the greatest changes in phenology were driven by assemblages of larger-bodied and shorter-distance migrants. This interpretation is consistent with other evidence that short-distance migrants are responding more readily to climate change (Butler 2003; Hurlbert & Liang 2012; La Sorte *et al.* 2016) and our finding that body mass explained the magnitude of phenological changes, with the most rapid advances occurring with an assemblage of larger-bodied birds supports this. In the western Gulf, where larger species, particularly waterfowl and shorebirds were more prevalent, the change in timing of passage at individual radar stations trended towards earlier passage times. Waterfowl species have been shown to have slightly higher incidences of advancing arrival dates on their breeding grounds in Canada compared to other taxa (Murphy-Klassen, Underwood, Sealy, & Czyrnyj, 2005). Longitudinal variation in the taxonomic composition of spring migrants along the north coast of the Gulf offers a unique opportunity to better understand how phenological responses to climate change vary among different categories of migrants (e.g. migration distance, winter range location, familial, etc.).

This study provides a long-term estimate of the total numbers of nocturnal migrant passing through the GOM region. Generating these estimates required a series of advances in radar processing and analytical methods (e.g. big data analytics for the entire radar archive), species occurrence information (eBird) and distribution modeling techniques (STEM), and in the procedures for calculating bird number through the integration of these resources and methods.

The characterization presented in this study represents a major leap forward for understanding the magnitude of bird migration in the Gulf region and brings us closer to achieving critical goals of monitoring in the region and understanding the role of migration in the dynamics of bird populations (Cohen et al., 2017). Our results from 2007-2015 did not show evidence of an overall decline in the number of migrating birds, however we did see evidence of a decline in the eastern Gulf. The lack of significant changes does not preclude the existence of troubling declines in the abundance of some migratory bird species during this time-period, especially aerial insectivores and migrants that breed in grasslands and coastal habitats (Environment and Climate Change Canada: Ottawa, Ontario., 2016; Nebel et al., 2010). However, it is possible that these observed declines are not evident in our findings due to increases in other species, which requires further study.

Synthesizing an increasing volume and diversity of ecological data to generate relevant and reliable summaries is a grand challenge in the natural sciences. Our methodology and results emphasize the importance of integrating WSR data with species-specific information (Horton et al., 2018; Kelly et al., 2016; La Sorte, Hochachka, Farnsworth, Sheldon, Fink, et al., 2015; La Sorte, Hochachka, Farnsworth, Sheldon, Van Doren, et al., 2015; Shipley, Kelly, & Frick, 2017). A common criticism of using WSR data to study the patterns and behaviors of migrating birds is the lack of species-specificity (Kelly & Horton, 2016). In this study, we present a path forward that can incorporate species-specific information with WSR data that that substantially enhances the scientific value of each individual dataset. However, our analysis, leveraging more than one million radar samples, is still a small fraction of the entirety of the radar archive, which totals 143 WSR stations (11 used in this study, 7.7%). Examining these questions at even larger extents

(e.g. continental United States) and across seasons (spring and fall) will increase our understanding of broad ecological consequences of a changing climate and bring us closer to a full-cycle analysis of migratory systems.

Our analysis of the timing and intensity of migration through the Gulf yields new insights necessary to address pressing global change research questions in a comprehensive and robust manner. For the first time, we can estimate where, when, and how many migrants move through this important ecological region. Our analysis showed that early migrants have advanced their movements through this region and mean body size and migrant distance was predictive of the pace of advancement. This adjustment should allow large-bodied migrants to time their arrival to the breeding grounds with changing resource phenology. However, the timing of peak migration movements has not changed, a period dominated by small long-distance songbirds which typically have less flexible migration programs (Berthold, 1996; Gwinner, 1996). While we did not detect declines over the duration of our study, this does not preclude the possibility that some declines are masked by increases in other species. This work fills a critical gap, enhancing our ability to document and understand existing consequences of global change. The resulting information is also important to inform modeling efforts designed to predict the long-term implications of different climate change scenarios and inform conservation efforts within the Gulf of Mexico region.

**Authors' contributions.** KGH, BVD, JFK, and AF worked to conceive and design this study. KGH, JK, and AF drafted the manuscript. KGH processed radar and wind data and generated

figures. KGH and BVD conducted and designed statistical analyses. DF designed and implemented the species distribution models, and FAL and DF designed the analysis of the model products. All the authors have provided editorial advice, approved the final version of this manuscript, and agree to be accountable for all aspects of the work.

**Acknowledgements:** We thank Cecilia Nilsson and Adriaan Dokter for comments and discussion on earlier drafts of this work. We would like to thank the eBird team for their support, and the many contributors to the eBird database. We thank Sidney Gauthreaux and one anonymous reviewer for providing constructive feedback. Funding for this project was provided by the Rose Postdoctoral Fellowship, Leon Levy Foundation, National Science Foundation (DBI-1661329; EF-1340921; IIS-1125098; ABI sustaining: DBI-1356308; ABI innovation: DBI-1661259; computing support from OCI-1053575 and DEB-110008), and Southern Company through their partnership with the National Fish and Wildlife Foundation.

## References:

- Askins, R. A., Lynch, J. F., & Greenberg, R. (1990). Population declines in migratory birds in eastern North America. *Current Ornithology*, 7, 1–57.
- Bairlein, F., & Winkel, W. (2001). Birds and climate change. In J. L. Lozán, H. Grafl, & P. Hupfer (Eds.), *Climate of the 21st century: changes and risks, scientific facts* (pp. 278–282). Hamburg, Germany.
- Berthold, P. (1996). *Control of bird migration*. London: Chapman and Hall.
- Both, C., Bouwhuis, S., Lessells, C. M., & Visser, M. E. (2006). Climate change and population declines in a long-distance migratory bird. *Nature*, 441(7089), 81–83.  
<https://doi.org/10.1038/nature04539>
- Both, C., & Visser, M. E. (2001). Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature*, 411(6835), 296. <https://doi.org/10.1038/35077063>
- Browning, K. A., & Wexler, R. (1968). The determination of kinematic properties of a wind field using Doppler radar. *Journal of Applied Meteorology*, 7, 105–113.
- Butler, C. J. (2003). The disproportionate effect of global warming on the arrival dates of short-distance migratory birds in North America. *Ibis*, 145(3), 484–495.  
<https://doi.org/10.1046/j.1474-919X.2003.00193.x>
- 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. *Scientific Reports*, 8(1), 3261. <https://doi.org/10.1038/s41598-018-21577-6>
- Calvert, A. M., Mackenzie, S. A., Flemming, J. M., Taylor, P. D., & Walde, S. J. (2012). Variation in songbird migratory behavior offers clues about adaptability to environmental change. *Oecologia*, 168(3), 849–861. <https://doi.org/10.1007/s00442-011-2119-5>



549 Chilson, P. B., Frick, W. F., Stepanian, P. M., Shipley, J. R., Kunz, T. H., & Kelly, J. F. (2012).  
 550 Estimating animal densities in the aerosphere using weather radar: To Z or not to Z?  
 551 *Ecosphere*, 3(8), art72. <https://doi.org/10.1890/ES12-00027.1>  
 552 Chrisman, J., N., & Ray, C. A. (2005). *A First Look at the Operational (Data Quality)*  
 553 *Improvements Provided by the Open Radar Data Acquisition (ORDA) System* (No.  
 554 P4R.10). Norman, OK, USA: Radar Operations Center (ROC).  
 555 Cimprich, D. A., & Moore, F. R. (1999). Energetic constraints and predation pressure during  
 556 stopover. In *Proceedings of the 22nd International Ornithological Congress* (pp. 834–  
 557 846). Johannesburg: BirdLife South Africa.  
 558 Cohen, E. B., Barrow, W. C., Buler, J. J., Deppe, J. L., Farnsworth, A., Marra, P. P., ... Moore,  
 559 F. R. (2017). How do en route events around the Gulf of Mexico influence migratory  
 560 landbird populations? *The Condor*, 119(2), 327–343. <https://doi.org/10.1650/CONDOR->  
 561 17-20.1  
 562 Cohen, E. B., Nemeth, Z., Zenzal Jr, T., Paxton, K., Diehl, R., Paxton, E., & Moore, F. (2015).  
 563 Spring resource phenology and timing of songbird migration across the Gulf of Mexico.  
 564 In E. M. Wood & J. L. Kellermann (Eds.), *In Phenological Synchrony and Bird*  
 565 *Migration: Changing Climate and Seasonal Resources in North America* (pp. 63–82).  
 566 Boca Raton, FL: CRC Press.  
 567 Cohen, J. M., Lajeunesse, M. J., & Rohr, J. R. (2018). A global synthesis of animal phenological  
 568 responses to climate change. *Nature Climate Change*, 8(3), 224–228.  
 569 <https://doi.org/10.1038/s41558-018-0067-3>

570 Cooper, N. W., Sherry, T. W., & Marra, P. P. (2015). Experimental reduction of winter food  
 571 decreases body condition and delays migration in a long-distance migratory bird.  
 572 *Ecology*, 96(7), 1933–1942. <https://doi.org/10.1890/14-1365.1>

573 Dokter, A. M., Liechti, F., Stark, H., Delobbe, L., Tabary, P., & Holleman, I. (2011). Bird  
 574 migration flight altitudes studied by a network of operational weather radars. *Journal of*  
 575 *The Royal Society Interface*, 8(54), 30–43. <https://doi.org/10.1098/rsif.2010.0116>

576 Dokter, Adriaan M., Farnsworth, A., Fink, D., Ruiz-Gutierrez, V., Hochachka, W. M., Sorte, F.  
 577 A. L., ... Kelling, S. (2018). Seasonal abundance and survival of North America's  
 578 migratory avifauna determined by weather radar. *Nature Ecology & Evolution*, 2(10),  
 579 1603–1609. <https://doi.org/10.1038/s41559-018-0666-4>

580 Dunning, J. B. J. (2008). *CRC handbook of avian body masses, Second Edition*. Boca Raton, FL.  
 581 Retrieved from [https://www.crcpress.com/CRC-Handbook-of-Avian-Body-Masses-](https://www.crcpress.com/CRC-Handbook-of-Avian-Body-Masses-Second-Edition/Dunning-Jr/p/book/9781420064445)  
 582 [Second-Edition/Dunning-Jr/p/book/9781420064445](https://www.crcpress.com/CRC-Handbook-of-Avian-Body-Masses-Second-Edition/Dunning-Jr/p/book/9781420064445)

583 Eastwood, E. (1967). *Radar Ornithology*. London, England: Methuen.

584 Environment and Climate Change Canada: Ottawa, Ontario. (2016). *North American Bird*  
 585 *Conservation Initiative* (The State of North America's Birds 2016) (pp. 1–8). Retrieved  
 586 from [www.stateofthebirds.org](http://www.stateofthebirds.org)

587 Farnsworth, A., Van Doren, B. M., Hochachka, W. M., Sheldon, D., Winner, K., Irvine, J., ...  
 588 Kelling, S. (2016). A characterization of autumn nocturnal migration detected by weather  
 589 surveillance radars in the northeastern US. *Ecological Applications*, 26(3), 752–770.  
 590 <https://doi.org/10.1890/15-0023>

591 Fink, D., Hochachka, W. M., Zuckerberg, B., Winkler, D. W., Shaby, B., Munson, M. A., ...  
 592 Kelling, S. (2010). Spatiotemporal exploratory models for broad-scale survey data.  
 593 *Ecological Applications*, 20(8), 2131–2147.

594 Gauthreaux, S. A., & Belser, C. G. (1998). Displays of bird movements on the WSR-88D:  
 595 patterns and quantification. *Weather and Forecasting*, 13, 453–464.

596 Gauthreaux, S. A., & Belser, C. G. (1999). Bird migration in the region of the Gulf of Mexico. In  
 597 N. J. Adams & R. H. Slotow (Eds.) (pp. 1931–1947). Durban: Birdlife South Africa.

598 Gauthreaux, S.A. (1992). The use of weather radar to monitor long-term patterns of trans-Gulf  
 599 migration in spring. In J. M. Hagen & D. W. Johnston (Eds.), *Ecology and conservation*  
 600 *of neotropical migrant landbirds* (pp. 96–100). Washington D.C.: Smithsonian Institution  
 601 Press.

602 Gauthreaux, Sidney A. (1971). A radar and direct visual study of passerine spring migration in  
 603 southern Louisiana. *Auk*, 88, 343–365.

604 Gienapp, P., & Bregnballe, T. (2012). Fitness Consequences of Timing of Migration and  
 605 Breeding in Cormorants. *PLOS ONE*, 7(9), e46165.  
 606 <https://doi.org/10.1371/journal.pone.0046165>

607 Gordo, O. (2007). Why are bird migration dates shifting? A review of weather and climate  
 608 effects on avian migratory phenology. *Climate Research*, 35, 37–58.  
 609 <https://doi.org/10.3354/cr00713>

610 Gwinner, E. (1996). Circannual clocks in avian reproduction and migration. *Ibis*, 138(1), 47–63.  
 611 <https://doi.org/10.1111/j.1474-919X.1996.tb04312.x>

612 Hahn, S., Bauer, S., & Liechti, F. (2009). The natural link between Europe and Africa – 2.1  
613 billion birds on migration. *Oikos*, 118(4), 624–626. <https://doi.org/10.1111/j.1600->  
614 0706.2008.17309.x

615 Hochachka, W. M., Fink, D., Hutchinson, R. A., Sheldon, D., Wong, W.-K., & Kelling, S.  
616 (2012). Data-intensive science applied to broad-scale citizen science. *Trends in Ecology*  
617 & *Evolution*, 27(2), 130–137. <https://doi.org/10.1016/j.tree.2011.11.006>

618 Horton, K. G., Van Doren, B., La Sorte, F. A., Fink, D., Sheldon, D., Farnsworth, A., & Kelly, J.  
619 F. (2018). Navigating north: how body mass and winds shape avian flight behaviors  
620 across a North American migratory flyway. *Ecology Letters*.

621 Horton, K. G., Van Doren, B. M., Stepanian, P. M., Farnsworth, A., & Kelly, J. F. (2016a).  
622 Seasonal differences in landbird migration strategies. *The Auk*, 133(4), 761–769.

623 Horton, K. G., Van Doren, B. M., Stepanian, P. M., Farnsworth, A., & Kelly, J. F. (2016b).  
624 Where in the air? Aerial habitat use of nocturnally migrating birds. *Biology Letters*,  
625 12(11), 20160591. <https://doi.org/10.1098/rsbl.2016.0591>

626 Horton, K. G., Van Doren, B. M., Stepanian, P. M., Hochachka, W. M., Farnsworth, A., & Kelly,  
627 J. F. (2016). Nocturnally migrating songbirds drift when they can and compensate when  
628 they must. *Scientific Reports*, 6, 21249. <https://doi.org/10.1038/srep21249>

629 Houghton, E. W., Blackwell, F., Ogilvie, M., & Wilmot, T. A. (1975). A radar study of wild  
630 ducks (pp. 41–84). Presented at the 10th Bird Strike Committee Europe Conference,  
631 Stockholm, Sweden: V. E. Ferry, ed.

632 Hüppop, O., & Winkel, W. (2006). Climate change and timing of spring migration in the long-  
633 distance migrant *Ficedula hypoleuca* in central

Europe: the role of spatially different temperature changes along migration routes.  
*Journal of Ornithology*, 147(2), 344–353. <https://doi.org/10.1007/s10336-005-0049-x>

Hurlbert, A. H., & Liang, Z. (2012). Spatiotemporal variation in avian migration phenology: citizen science reveals effects of climate change. *PLoS ONE*, 7(2), e31662.  
<https://doi.org/10.1371/journal.pone.0031662>

Jonzén, N., Lindén, A., Ergon, T., Knudsen, E., Vik, J. O., Rubolini, D., ... Stenseth, N. C. (2006). Rapid Advance of Spring Arrival Dates in Long-Distance Migratory Birds. *Science*, 312(5782), 1959–1961. <https://doi.org/10.1126/science.1126119>

Kelling, S., Hochachka, W. M., Fink, D., Riedewald, M., Caruana, R., Ballard, G., & Hooker, G. (2009). Data-intensive Science: A New Paradigm for Biodiversity Studies. *BioScience*, 59(7), 613–620. <https://doi.org/10.1525/bio.2009.59.7.12>

Kelly, J. F., & Horton, K. G. (2016). Toward a predictive macrosystems framework for migration ecology. *Global Ecology and Biogeography*, 25, 1159–1165.  
<https://doi.org/10.1111/geb.12473>

Kelly, J. F., Horton, K. G., Stepanian, P. M., de Beurs, K. M., Fagin, T., Bridge, E. S., & Chilson, P. B. (2016). Novel measures of continental-scale avian migration phenology related to proximate environmental cues. *Ecosphere*, 7(8), 1–13.  
<https://doi.org/10.1002/ecs2.1434>

La Sorte, F. A., Fink, D., Buler, J. J., Farnsworth, A., & Cabrera-Cruz, S. A. (2017). Seasonal associations with urban light pollution for nocturnally migrating bird populations. *Global Change Biology*, 23(11), 4609–4619. <https://doi.org/10.1111/gcb.13792>

La Sorte, F. A., Fink, D., Hochachka, W. M., Farnsworth, A., Rodewald, A. D., Rosenberg, K. V., ... Kelling, S. (2014). The role of atmospheric conditions in the seasonal dynamics of

657 North American migration flyways. *Journal of Biogeography*, 41(9), 1685–1696.  
658 <https://doi.org/10.1111/jbi.12328>

659 La Sorte, F. A., Hochachka, W. M., Farnsworth, A., Dhondt, A. A., & Sheldon, D. (2016). The  
660 implications of mid-latitude climate extremes for North American migratory bird  
661 populations. *Ecosphere*, 7(3). <https://doi.org/10.1002/ecs2.1261>

662 La Sorte, F. A., Hochachka, W. M., Farnsworth, A., Sheldon, D., Fink, D., Geevarghese, J., ...  
663 Kelling, S. (2015). Migration timing and its determinants for nocturnal migratory birds  
664 during autumn migration. *Journal of Animal Ecology*, 84(5), 1202–1212.  
665 <https://doi.org/10.1111/1365-2656.12376>

666 La Sorte, F. A., Hochachka, W. M., Farnsworth, A., Sheldon, D., Van Doren, B., Fink, D., &  
667 Kelling, S. (2015). Seasonal changes in the altitudinal distribution of nocturnally  
668 migrating birds during autumn migration. *Royal Society Open Science*, 2(12), 150347.  
669 <https://doi.org/10.1098/rsos.150347>

670 Larkin, R. P. (1991). Flight speeds observed with radar, a correction: slow “birds” are insects.  
671 *Behavioral Ecology and Sociobiology*, 29, 221–224.

672 Liaw, A., & Wiener, M. (2002). Classification and Regression by randomForest. *R News*, 2(3),  
673 18–22.

674 Loss, S. R., Will, T., Loss, S. S., & Marra, P. P. (2014). Bird–building collisions in the United  
675 States: Estimates of annual mortality and species vulnerability. *The Condor*, 116(1), 8–  
676 23. <https://doi.org/10.1650/CONDOR-13-090.1>

677 Loss, S. R., Will, T., & Marra, P. P. (2013a). Estimates of bird collision mortality at wind  
678 facilities in the contiguous United States. *Biological Conservation*, 168, 201–209.  
679 <https://doi.org/10.1016/j.biocon.2013.10.007>

680 Loss, S. R., Will, T., & Marra, P. P. (2013b). The impact of free-ranging domestic cats on  
 681 wildlife of the United States. *Nature Communications*, 4, 1396.  
 682 <https://doi.org/10.1038/ncomms2380>  
 683 Lowery, G. H. (1946). Evidence of trans-Gulf migration. *The Auk*, 63, 175–210.  
 684 Marra, P. P., Francis, C. M., Mulvihill, R. S., & Moore, F. R. (2005). The influence of climate on  
 685 the timing and rate of spring bird migration. *Oecologia*, 142(2), 307–315.  
 686 <https://doi.org/10.1007/s00442-004-1725-x>  
 687 Mayor, S. J., Guralnick, R. P., Tingley, M. W., Otegui, J., Withey, J. C., Elmendorf, S. C., ...  
 688 Schneider, D. C. (2017). Increasing phenological asynchrony between spring green-up  
 689 and arrival of migratory birds. *Scientific Reports*, 7. [https://doi.org/10.1038/s41598-017-](https://doi.org/10.1038/s41598-017-02045-z)  
 690 [02045-z](https://doi.org/10.1038/s41598-017-02045-z)  
 691 McLaren, J. D., Buler, J. J., Schreckengost, T., Smolinsky, J. A., Boone, M., Loon, E. E. van, ...  
 692 Walters, E. L. (2018). Artificial light at night confounds broad-scale habitat use by  
 693 migrating birds. *Ecology Letters*, 21(3), 356–364. <https://doi.org/10.1111/ele.12902>  
 694 Mesinger, F., DiMego, G., Kalnay, E., Mitchell, K., Shafran, P. C., Ebisuzaki, W., ... Shi, W.  
 695 (2006). North American Regional Reanalysis. *Bulletin of the American Meteorological*  
 696 *Society*, 87(3), 343–360. <https://doi.org/10.1175/BAMS-87-3-343>  
 697 Møller, Anders P., Balbontín, J., Cuervo, J. J., Hermosell, I. G., & de Lope, F. (2009). Individual  
 698 differences in protandry, sexual selection, and fitness. *Behavioral Ecology*, 20(2), 433–  
 699 440. <https://doi.org/10.1093/beheco/arn142>  
 700 Møller, Anders Pape, Fiedler, W., & Berthold, P. (Eds.). (2010). *Effects of Climate Change on*  
 701 *Birds*. OUP Oxford.

702 Møller, Anders Pape, Rubolini, D., & Lehikoinen, E. (2008). Populations of migratory bird  
 703 species that did not show a phenological response to climate change are declining.  
 704 *Proceedings of the National Academy of Sciences*, 105(42), 16195–16200.  
 705 <https://doi.org/10.1073/pnas.0803825105>  
 706 Moore, F. R. (2018). Biology of landbird migrants: a stopover perspective. *The Wilson Journal*  
 707 *of Ornithology*, 130(1), 1–12. <https://doi.org/10.1676/1559-4491-130.1.1>  
 708 Murphy-Klassen, H. M., Underwood, T. J., Sealy, S. G., & Czyrnyj, A. A. (2005). Long-Term  
 709 Trends in Spring Arrival Dates of Migrant Birds at Delta Marsh, Manitoba, in Relation to  
 710 Climate Change (Tendances à Long-terme des Dates d'Arrivée Printanières des Oiseaux  
 711 Migrateurs dans le Delta Marsh, Manitoba, en Relation avec les Changements  
 712 Climatiques). *The Auk*, 122(4), 1130–1148.  
 713 Nebel, S., Mills, A., McCracken, J., & Taylor, P. (2010). Declines of Aerial Insectivores in  
 714 North America Follow a Geographic Gradient. *Avian Conservation and Ecology*, 5(2).  
 715 <https://doi.org/10.5751/ACE-00391-050201>  
 716 Newton, I. (2003). *The Speciation and Biogeography of Birds*. Gulf Professional Publishing.  
 717 Norris, D. R., & Marra, P. P. (2007). Seasonal interactions, habitat quality, and population  
 718 dynamics in migratory birds. *The Condor*, 109, 535–547.  
 719 Norris, D. Ryan, Marra, P. P., Kyser, T. K., Sherry, T. W., & Ratcliffe, L. M. (2004). Tropical  
 720 winter habitat limits reproductive success on the temperate breeding grounds in a  
 721 migratory bird. *Proceedings of the Royal Society of London B: Biological Sciences*,  
 722 271(1534), 59–64. <https://doi.org/10.1098/rspb.2003.2569>  
 723 Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts  
 724 across natural systems. *Nature*, 421(6918), 37–42. <https://doi.org/10.1038/nature01286>



725 Rich, T. D., Beardmore, C. J., Berlanga, H., Blancher, P. J., Bradstreet, M. S. W., Butcher, G. S.,  
 726 ... Will, T. C. (2004). *Partners in Flight North American Landbird Conservation Plan*.  
 727 Ithaca, NY: Cornell Lab of Ornithology.

728 Ridgely, R. S., Allnutt, T. F., Brooks, T., McNicol, D. K., Mehlman, D. W., Young, B. E., &  
 729 Zook, J. R. (2007). Digital distribution maps of the birds of the Western Hemisphere  
 730 (Version version 3.0). Arlington, Virginia, USA: NatureServe.

731 Robbins, C. S., Sauer, J. R., Greenberg, R. S., & Droege, S. (1989). Population declines in North  
 732 American birds that migrate to the Neotropics. *Proceedings of the National Academy of*  
 733 *Sciences; (USA)*, 86, 7658–7662.

734 Sahr, K. (2011). Hexagonal discrete global GRID systems for geospatial computing. *Archives of*  
 735 *Photogrammetry, Cartography and Remote Sensing*, (Vol. 22), 363--376.

736 Sahr, Kevin, White, D., & Kimerling, A. J. (2003). Geodesic Discrete Global Grid Systems.  
 737 *Cartography and Geographic Information Science*, 30(2), 121–134.  
 738 <https://doi.org/10.1559/152304003100011090>

739 Saino, N., Rubolini, D., Jonzén, N., Ergon, T., Montemaggiore, A., Stenseth, N. C., & Spina, F.  
 740 (2007). Temperature and rainfall anomalies in Africa predict timing of spring migration  
 741 in trans-Saharan migratory birds. *Climate Research*, 35(1–2), 123–134.  
 742 <https://doi.org/10.3354/cr00719>

743 Schmaljohann, H., & Both, C. (2017). The limits of modifying migration speed to adjust to  
 744 climate change. *Nature Climate Change*, 7(8), 573–576.  
 745 <https://doi.org/10.1038/nclimate3336>

746 Sheldon, D. (2015). *WSRLIB: MATLAB toolbox for weather surveillance radar*. Retrieved from  
 747 <http://bitbucket.org/dsheldon/wsrlib>

748 Sheldon, D., Farnsworth, A., Irvine, J., Van Doren, B., Webb, K., Dietterich, T. G., & Kelling, S.  
 749 (2013). Approximate Bayesian inference for reconstructing velocities of migrating birds  
 750 from weather radar. *Association for the Advancement of Artificial Intelligence*, 1334–  
 751 1340.

752 Shipley, J. R., Kelly, J. F., & Frick, W. F. (2017). Toward integrating citizen science and radar  
 753 data for migrant bird conservation. *Remote Sensing in Ecology and Conservation*, 0(0).  
 754 <https://doi.org/10.1002/rse2.62>

755 Smith, R. J., & Moore, F. R. (2005). Arrival timing and seasonal reproductive performance in a  
 756 long-distance migratory landbird. *Behavioral Ecology and Sociobiology*, 57, 231–239.

757 Stepanian, P. M., Horton, K. G., Melnikov, V. M., Zrnić, D. S., & Gauthreaux, S. A. (2016).  
 758 Dual-polarization radar products for biological applications. *Ecosphere*, 7(11), 1–27.  
 759 <https://doi.org/10.1002/ecs2.1539>

760 Stevenson, H. M. (1957). The relative magnitude of the trans-Gulf and circum-Gulf spring  
 761 migrations. *Wilson Bulletin*, (69), 39–77.

762 Strode, P. K. (2003). Implications of climate change for North American wood warblers  
 763 (Parulidae). *Global Change Biology*, 9(8), 1137–1144. [https://doi.org/10.1046/j.1365-](https://doi.org/10.1046/j.1365-2486.2003.00664.x)  
 764 [2486.2003.00664.x](https://doi.org/10.1046/j.1365-2486.2003.00664.x)

765 Strode, P. K. (2009). Spring Tree Species Use by Migrating Yellow-Rumped Warblers in  
 766 Relation to Phenology and Food Availability. *The Wilson Journal of Ornithology*, 121(3),  
 767 457–468. <https://doi.org/10.1676/05-148.1>

768 Strode, P. K. (2015). Phenological asynchrony between migrant songbirds and food resources  
 769 during early springs: initiation of a trophic cascade at a stopover site. In E. M. Wood & J.

- L. Kellermann (Eds.), *Phenological synchrony and bird migration: changing climate and seasonal resources in North America* (pp. 97–116). Studies in Avian Biology.
- Studds, C. E., & Marra, P. P. (2011). Rainfall-induced changes in food availability modify the spring departure programme of a migratory bird. *Proceedings. Biological Sciences*, 278(1723), 3437–3443. <https://doi.org/10.1098/rspb.2011.0332>
- Sullivan, B. L., Aycrigg, J. L., Barry, J. H., Bonney, R. E., Bruns, N., Cooper, C. B., ... Kelling, S. (2014). The eBird enterprise: an integrated approach to development and application of citizen science. *Biological Conservation*, 169, 31–40. <https://doi.org/10.1016/j.biocon.2013.11.003>
- Thackeray, S. J., Henrys, P. A., Hemming, D., Bell, J. R., Botham, M. S., Burthe, S., ... Wanless, S. (2016). Phenological sensitivity to climate across taxa and trophic levels. *Nature*, 535(7611), 241–245. <https://doi.org/10.1038/nature18608>
- Usui, T., Butchart, S. H. M., & Phillimore, A. B. (2017). Temporal shifts and temperature sensitivity of avian spring migratory phenology: a phylogenetic meta-analysis. *Journal of Animal Ecology*, 86(2), 250–261. <https://doi.org/10.1111/1365-2656.12612>
- Van Doren, B. M., & Horton, K. G. (2018). A continental system for forecasting bird migration. *Science*, 361(6407), 1115–1118. <https://doi.org/10.1126/science.aat7526>
- 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. *Proceedings of the National Academy of Sciences*, 114(42), 11175–11180. <https://doi.org/10.1073/pnas.1708574114>

791 Visser, M. E., Perdeck, A. C., Balen, J. H. V., & Both, C. (2009). Climate change leads to  
 792 decreasing bird migration distances. *Global Change Biology*, 15(8), 1859–1865.  
 793 <https://doi.org/10.1111/j.1365-2486.2009.01865.x>

794 Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., ... Bairlein, F.  
 795 (2002). Ecological responses to recent climate change. *Nature*, 416(6879), 389–395.  
 796 <https://doi.org/10.1038/416389a>

797 Wood, E. M., & Pidgeon, A. M. (2015). Extreme variations in spring temperature affect  
 798 ecosystem regulating services provided by birds during migration. *Ecosphere*, 6(11),  
 799 art216. <https://doi.org/10.1890/ES15-00397.1>

800 Wood, E. M., Pidgeon, A. M., Liu, F., & Mladenoff, D. J. (2012). Birds see the trees inside the  
 801 forest: The potential impacts of changes in forest composition on songbirds during spring  
 802 migration. *Forest Ecology and Management*, 280, 176–186.  
 803 <https://doi.org/10.1016/j.foreco.2012.05.041>  
 804

**Figure Captions:**

**Figure 1:** Locations of weather surveillance radar (WSR) stations and segments used for calculating nocturnal migration traffic through the Gulf of Mexico region. WSR stations were categorized into three regions, western (KCRP, KBRO, KHGX), central (KLCH, KLIX, KMOB, KEVX), and eastern (KTLH, KTBW, KBYX, KAMX), listed by increasing longitude. Stations and segments are shaded by longitude.

**Figure 2:** (a) Radar cross-section ( $\text{cm}^2$ ) relationship with average species body mass (gram). Body masses derived from Dunning (2008) and radar cross-sections from Eastwood (1967) and Houghton et al. (1975). (b) Average body mass (gram, log-scale) of nocturnal species by order and their corresponding radar cross-section (RCS,  $\text{cm}^2$ , log-scale) as predicted by (a). The number of species within each order is shown in parentheses.

**Figure 3:** (a) Spring proportional occurrence of the top three species-rich orders in the western, central, and eastern regions. (b) Mean mass (g) and predicted radar cross-section ( $\text{cm}^2$ ) for each region based on body mass weighted by STEM probability of occurrence. (c) Mean migration distance (m) for each region weighted by STEM probability of occurrence. Lines of (a-c) were generated by generalized additive models. Shaded regions show 95% confidence intervals from generalized additive models.

**Figure 4:** (a) Average cumulative number of nocturnal migrants passing through the northern Gulf of Mexico region from 2007 to 2015. Upper and lower lines show the standard error of generalized additive model. Dotted line and dates show the point at which 25, 50, and 75% of the

migrants have passed. (b) Average seasonal phenology of the number of migrants passing each weather surveillance (WSR) station from 2007 to 2015. Inset shows the mean seasonal activity with disk size scaled to the square-root of the mean traffic rate (bird km<sup>-1</sup>). (c-e) Cumulative proportion of migrants passing through the western, central and eastern regions. Individual lines represent years for each WSR station from 1995 to 2015. Dates shows the average point at which 50% of the migrants have passed and the black and gray bars show one and two standard deviations, respectively. Lines and points are shaded by WSR station longitude.

**Figure 5:** (a) Per year percent change in cumulative nocturnal migrant traffic rate from 2007-2015 for each weather surveillance radar (WSR) station. Error bars and average regional percent change shown with standard error. Inset reshown to emphasize the geographic disparity in traffic intensity. (b) Change in migration timing (days decade<sup>-1</sup>) from 1995-2015 by body mass (grams) and migrant distance (m) derived by eBird species probabilities of occurrence. Fitted lines shown from a linear mixed-effects model with WSR station as a random effect and the 95% confidence interval from 1000 bootstrapped samples. Predictions only plotted for ranges for which observations were represented in our dataset.

**Graphical Abstract:** We quantify the timing, intensity, and distribution of bird migration through one of the largest migration corridors in the Western Hemisphere, the Gulf of Mexico, by integrating citizen science (eBird) observations with weather surveillance radar data. We estimate that an average of 2.1 billion birds pass through this region each spring, with half of these individuals pass through the region in just 18 days, between April 19<sup>th</sup> and May 7<sup>th</sup>. We did not detect an overall change in the annual numbers of migrants (2007-2015) or the annual timing

851 of peak migration (1995-2015).