

Holding steady: Little change in intensity or timing of bird migration over the Gulf of Mexico

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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 whether 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 and May 7. 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⁻¹). 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.

KEYWORDS

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

1 | 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 (Van Doren & Horton, 2018; Gauthreaux, 1971; Horton, Van Doren, Stepanian, Hochachka, et al., 2016) 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; Van Doren et al., 2017; McLaren et al., 2018; La Sorte, Fink, Buler, Farnsworth, & Cabrera-Cruz, 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 stop-over 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 & Winkler, 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., Gienapp & Bregnballe, 2012; Møller, Balbontín, Cuervo, Hermosell, & Lope, 2009; Smith & Moore, 2005). 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 broadscale 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 macroscale movements (Horton et al., 2018; Kelly et al., 2016; La Sorte, Hochachka, Farnsworth, Sheldon, Van Doren, et al., 2015; La Sorte, Hochachka, Farnsworth, Sheldon, Fink, 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 multidimensional 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 (a) timing, (b) intensity, (c) distribution, and (d) 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).

2 | MATERIALS AND METHODS

2.1 | Weather surveillance radar

2.1.1 | Data processing

We used unfiltered (i.e., level-II) weather surveillance radar data from 11 stations surrounding the Gulf (Figure 1), acquired from NOAA's National Centers for Environmental Information, for the period March 1 to May 31 for each year from 1995 to 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 ground-speed from radial velocity following Browning and Wexler (1968) and migration traffic from reflectivity from 0 to 3,000 m above ground level (a.g.l.), at 100 m altitudinal bins, following Farnsworth et al. (2016) and Horton, Van Doren, Stepanian, Farnsworth, and Kelly (2016b). We constructed height profiles of migrant track and intensity from the lowest elevation sweeps ($0.5\text{--}4.5^\circ$) from 5 to

37.5 km. Elevation sweeps are completed every 5–10 min, 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) <1 , and we removed samples with RMSE >5 to limit poor fits (Dokter et al., 2011; Horton, Van Doren, Stepanian, Farnsworth, & Kelly, 2016a; Horton, Van Doren, Stepanian, Hochachka, et al., 2016). We used samples with northward tracks only ($<90^\circ$ and $>270^\circ$, Figure S1), resulting in an elimination of 14.1% of the data that remained after filtering protocols.

2.1.2 | 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°), starting on March 1 (00:00 UTC) and selected every 5th scan (day and night). We classified any pixel above the 85th 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.

2.1.3 | 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.,

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

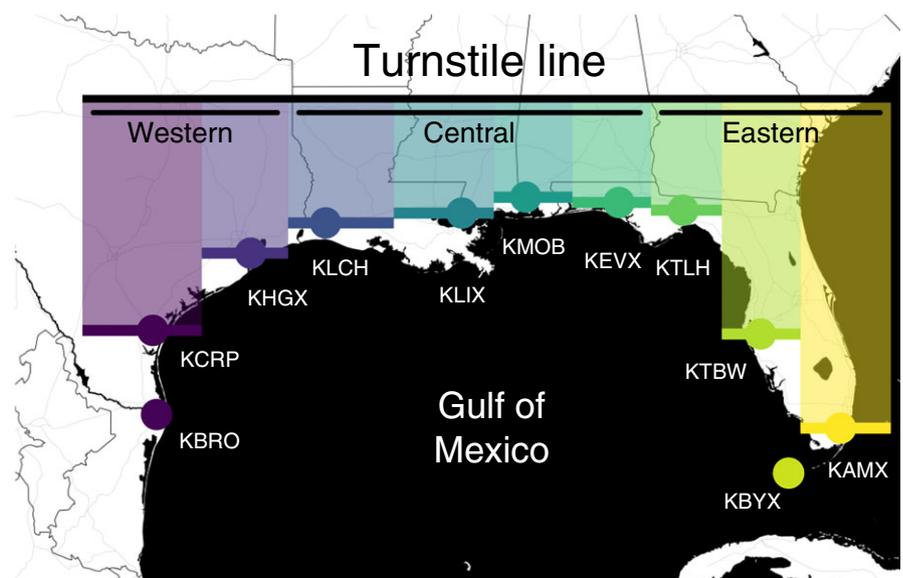


Figure S2), independently classified by KGH and BVD. We used samples with common classification agreement in the training set (93.7% of scans). We randomly selected scans for the training set in sequence sets for each radar for each year (mean samples per radar 102 year^{-1}). We extracted derived predictor 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 1,000 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.

2.1.4 | Insect mitigation

To limit insect contamination, we eliminated data from height bins with airspeeds $< 5 \text{ m/s}$ (Van Doren & Horton, 2018; Gauthreaux & Belser, 1998; Larkin, 1991). 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) dataset (Mesinger et al., 2006). NARR models zonal and meridional wind components every 3 hr at 25 hPa increments at a gridded 32-km spatial resolution. We aligned the nearest radar measures by time and height above ground level.

2.2 | 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 > 0 in our sampling area (see Table S3). STEM use underlying landscape (land cover, 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 ($\leq 8.1 \text{ km}$) with local start times between 05:00 and 20:00 and counts that were $< 3 \text{ hr}$ in duration. We rendered weekly estimates of probability of occurrence for each species at 130,751 points at a density of *ca.* 15 per $30 \times 30 \text{ km}$ within the contiguous United States 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 80th percentile of the nonzero occurrence probabilities for that week, and if the 80th percentile was < 0.0175 , which defined our minimum probability threshold, the probability threshold was set to 0.0175.

2.3 | Migrant distance

To estimate migrant distance, we used NatureServe breeding and nonbreeding 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, White, & Kimerling, 2003). Following this step, total migration distance was calculated as the great circle (orthodromic) distance between the geographic centroids of the breeding and nonbreeding ranges for each species. Geographic centroids were estimated by averaging the geographic locations of the hexagon cell centers occurring within each species' breeding and nonbreeding 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.

2.4 | Estimating the number of migrants

To estimate the number of migrants passing, we first converted reflectivity factor (dBZ) to reflectivity (dB η) 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 (λ) 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 (η) resulted in units of $\text{cm}^2 \text{ km}^{-3}$. We converted reflectivity (η) to birds 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 km^{-3} by the northward component of the measured groundspeed (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 km^{-2} . We multiplied by the altitudinal resolution (0.1 km) of each altitudinal bin, resulting in birds 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 is limited. For this reason, we used previously measured S-band ($\sim 10 \text{ cm}$ 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, nonlinear relationship between RCS and reflector size (Stepanian, Horton, Melnikov, Zmić, & 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 ($\log_{10}(\text{cross-section}) = 0.670 \log_{10}(\text{body mass})$, $p < 0.001$, $df = 10$, Figure 2a). Using this relationship, we converted the average mass of each species likely to pass through the region to a species-specific RCS (Figure 2b, Table S3).

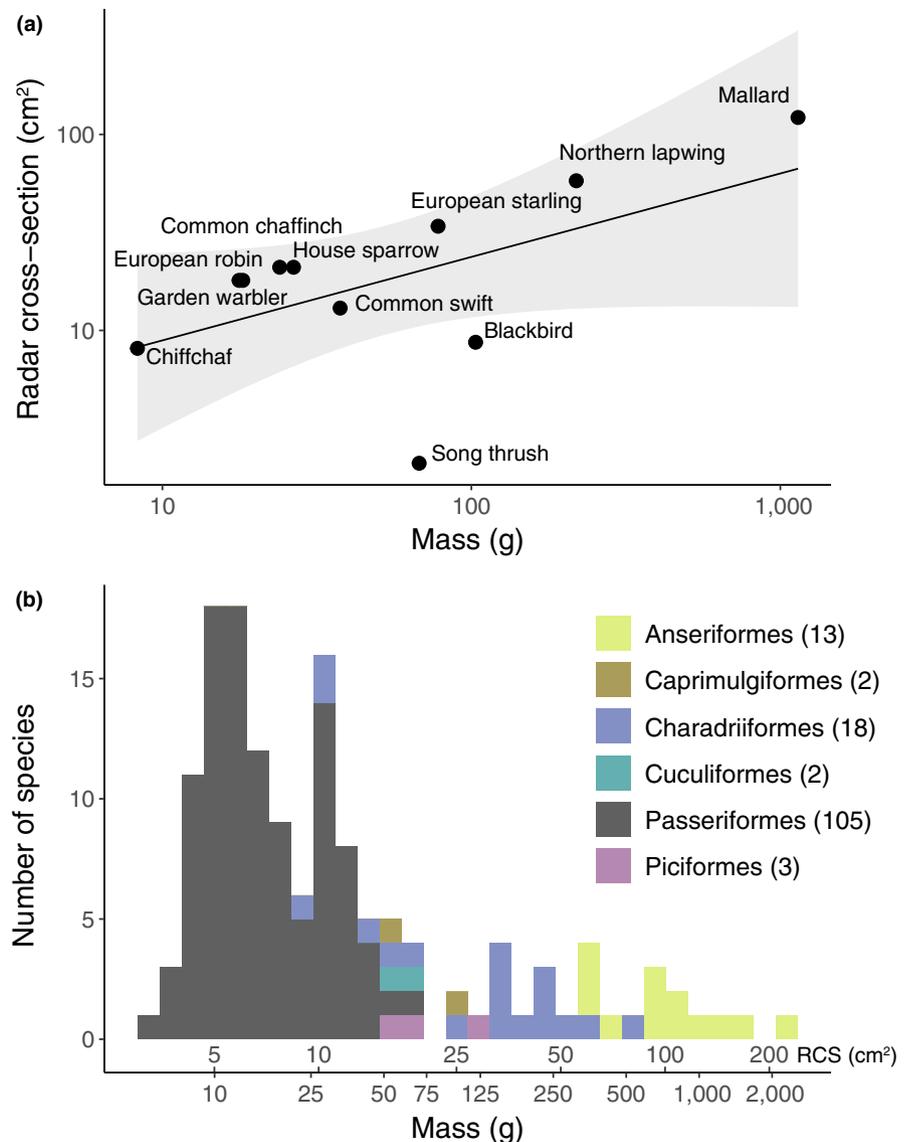


FIGURE 2 (a) Radar cross-section (cm²) relationship with average species body mass (g). Body masses derived from Dunning (2008) and radar cross-sections from Eastwood (1967) and Houghton et al. (1975). (b) Average body mass (gram, log-scale) of nocturnal species by order and their corresponding radar cross-section (RCS, cm², log-scale) as predicted by (a). The number of species within each order is shown in parentheses

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 (GAM) 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, Figure 1). We determined individual radar segments by measuring the distance between the midpoints of the radar locations. Multiplying the northward component of bird traffic at each station (birds km⁻¹) 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

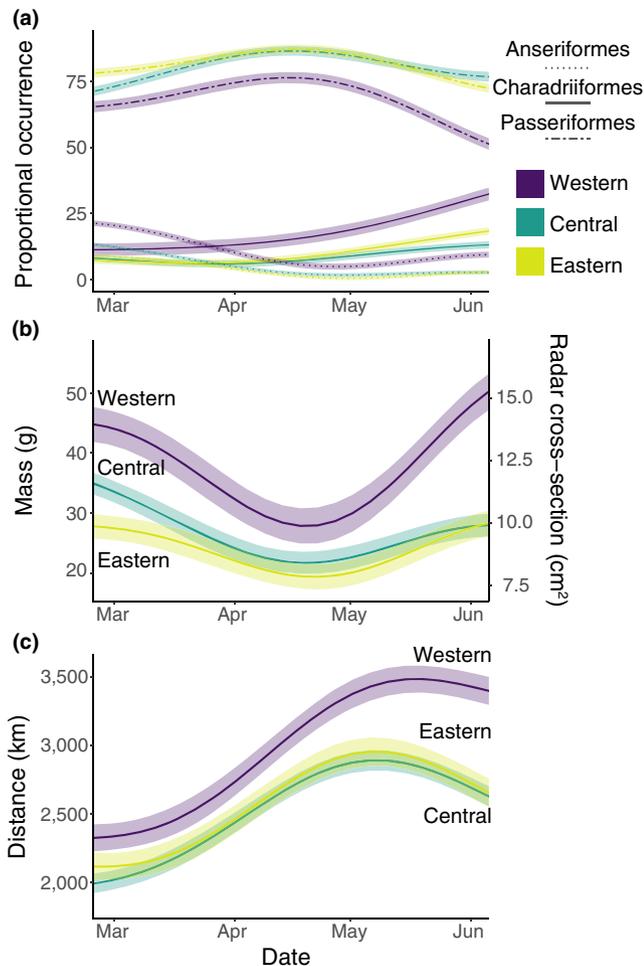


FIGURE 3 (a) Spring proportional occurrence of the top three species-rich orders in the western, central, and eastern regions. (b) Mean mass (g) and predicted radar cross-section (cm²) for each region based on body mass weighted by STEM probability of occurrence. (c) Mean migration distance (km) for 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

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.

2.5 | 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 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 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 contaminated 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: (a) nights with precipitation were more likely to have low bird densities and (b) nights with precipitation were 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 whether 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 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 Figure 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 whether 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 1,000 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 (1995–2015) to make phenological estimates, because they are insensitive to these changes.

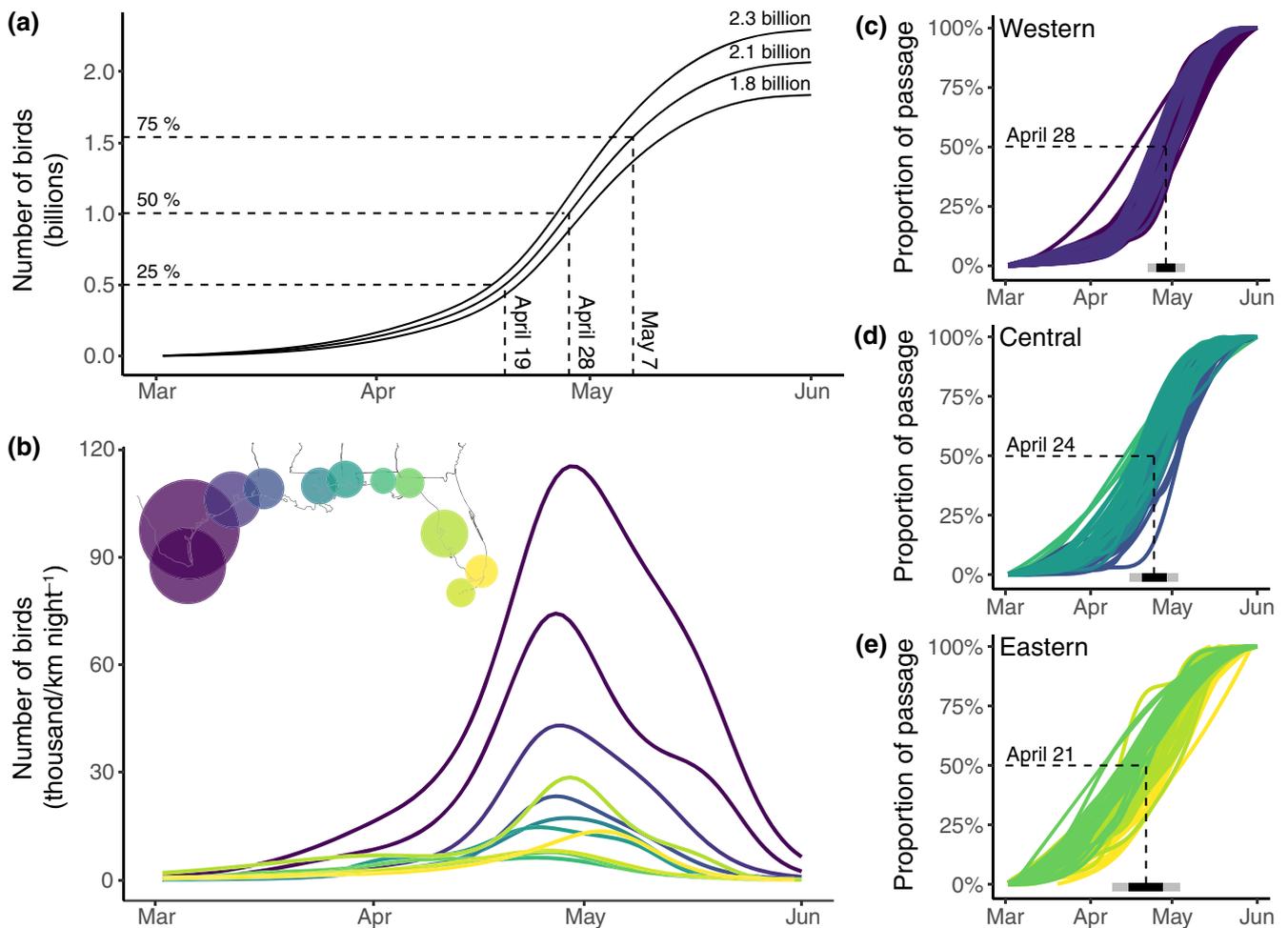


FIGURE 4 (a) Average cumulative number of nocturnal migrants passing through the northern Gulf of Mexico region from 2007 to 2015. Upper and lower lines show the standard error of generalized additive model. Dotted line and dates show the point at which 25%, 50%, and 75% of the migrants have passed. (b) Average seasonal phenology of the number of migrants passing per night at 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^{-1}). (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 show 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

3 | 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 (Figure 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 cm^2 (18.1 g) and 19.5 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 (Figure 3b). Assemblage migratory distance generally increased through the season and was highest in the western region (Figure 3c).

Integrating species observations with radar measures, we estimated an average of 2.1 ± 0.2 (SE) billion migrants pass through the Gulf region during spring migration (range 1.7–2.6, Figure 4a, Figure 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 (Figure 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 (Figure 4b). The western region had an average migration rate of $26,224 \text{ bird km}^{-1}\text{night}^{-1}$, 5.4 times higher than the central and eastern regions (Figure 4b). Half of the migrants passing the Gulf region passed in an 18-day period between April 19 and May 7 (Figure 4a). Site-specific patterns of phenology were similar across the region,

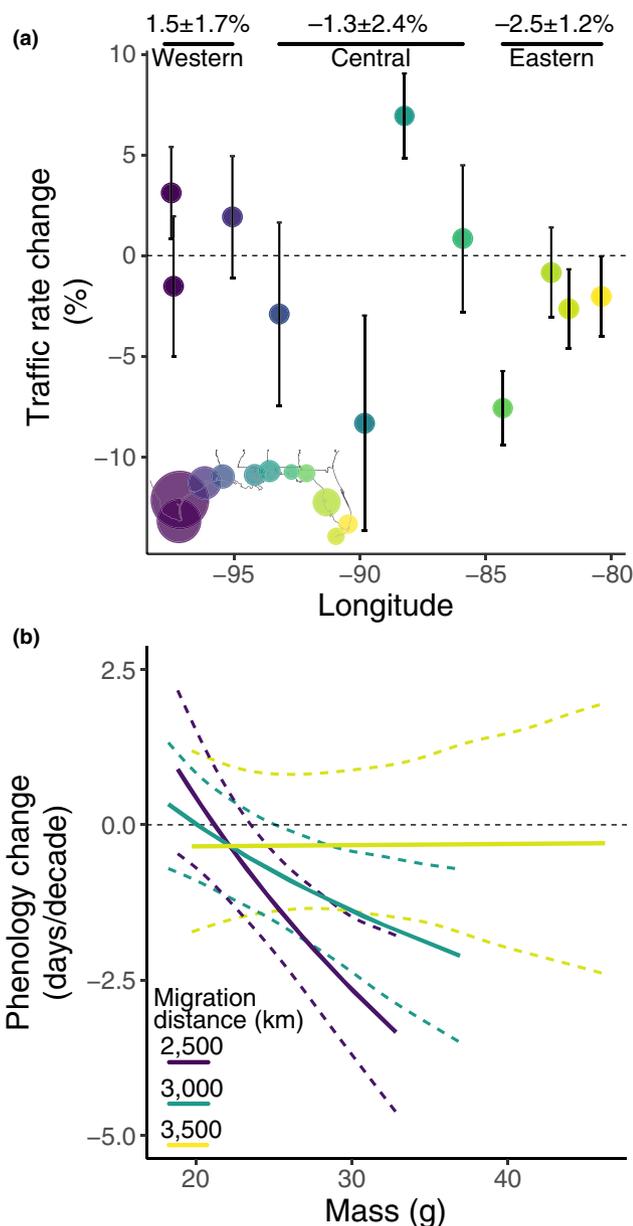


FIGURE 5 (a) Per year percent change in cumulative nocturnal migrant traffic rate from 2007 to 2015 for each weather surveillance radar (WSR) station. Error bars and average regional percent change shown with standard error. Inset reshown to emphasize the geographic disparity in traffic intensity. (b) Change in migration timing (days decade⁻¹) from 1995 to 2015 by body mass (g) and migrant distance (km) 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 1,000 bootstrapped samples. Predictions only plotted for ranges for which observations were represented in our dataset

with peaks in late April and early May (Figure 4b). However, we generally observed earlier and more variable peak dates moving eastward across the Gulf region (Figure 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 (Figure 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 ($-2.5 \pm 1.2\%$ year⁻¹ SE, $p = 0.033$).

From 1995 to 2015, we observed a significant advancement (1.6 ± 0.7 days decade⁻¹ SE, $p = 0.035$) in the timing of early-season migratory movements (i.e., 5% of cumulative movement, Figure S6); however, we did not see significant changes for later periods (25th, $p = 0.518$; 50th, $p = 0.588$; 75th, $p = 0.599$, 95th, $p = 0.638$, Figure 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 shorter-distance migrants (Figure 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 ($p = 0.015$, Figure S6).

4 | 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 ± 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 and May 7, 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 2–3 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⁻¹ 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 toward 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, and foraging guild).

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 to 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 (Nebel et al., 2010; The State of North America's Birds, 2016). 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; Shipley, Kelly, & Frick, 2017; La Sorte, Hochachka, Farnsworth, Sheldon, Fink, et al., 2015; La Sorte, Hochachka, Farnsworth, Sheldon, Fink, et al., 2015). 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 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 annual-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 (Bertold, 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.

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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.

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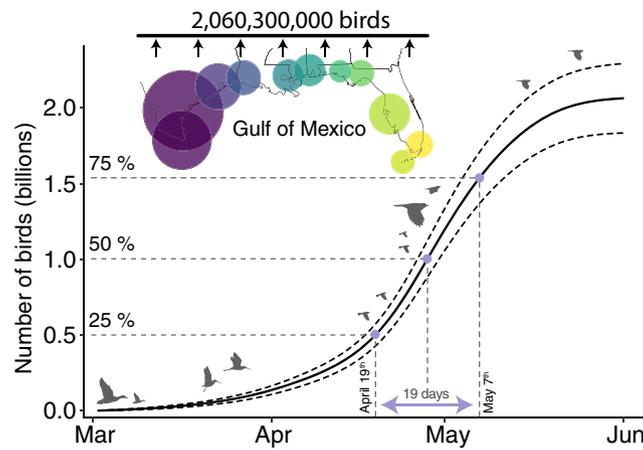
SUPPORTING INFORMATION

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Graphical Abstract

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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 and May 7. We did not detect an overall change in the annual numbers of migrants (2007–2015) or the annual timing of peak migration (1995–2015).