Wrecked: Impacts of Atlantic Tropical Cyclones on Neotropical Bird Migrants

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Executive Summary

North American birds are under pressure. With nearly 3 billion birds lost in the last half century (Rosenberg et al., 2019), understanding and quantifying incremental avian mortality is vital. There are many perils for birds that migrate from their breeding grounds in the mid and high latitudes of the continent to their wintering grounds in the Neotropics, including Atlantic tropical cyclones that birds can encounter as they cross through some of the busy hurricane corridors of the Gulf of Mexico, Caribbean, and western North Atlantic. The aim of my research is to provide the first comprehensive measure of the effect of Atlantic tropical cyclone activity on bird migration intensity by testing whether active hurricane seasons may cause a significant reduction in the number of Neotropical migrants.

I used weather surveillance radars spanning the Gulf of Mexico to determine bird migration intensity from 1995 to 2018. I employed a dataset for which artificial intelligence processes separated avian targets from precipitation and background interference and that included an estimate of total seasonal bird passage. I determined the level of tropical cyclone activity from the Accumulated Cyclone Energy (ACE) index. To establish whether there was a relation between tropical cyclone activity and migrants, I used generalized additive mixed-effects models to test spring bird passage as a function of ACE during the peak of the fall migration season. I did this first with ACE extracted for the entire Atlantic basin and subsequently for subregions of the Atlantic (e.g., Gulf of Mexico and the Caribbean), and compared all models.

I found a strong negative relationship between tropical cyclone activity in the Atlantic basin and the subsequent spring's migrant bird passage. When there were more storms and/or stronger hurricanes across the whole North Atlantic Ocean during the peak of the fall migration between August and November, fewer birds returned the following spring. Specifically, there

was a predicted decrease of 21.8% in the number of birds crossing the Gulf during springs following the most active Atlantic hurricane seasons compared to the least active seasons. While this finding might imply that storms directly impacted birds, a more granular examination of the data suggests other possibilities. The relationship between storm activity and spring bird passage was much weaker in the Gulf of Mexico and the Caribbean compared to the open Atlantic, even though more bird migration occurs in those areas. Instead, the negative association between storm activity and migration traffic may reflect a link between the short-term climatic variability that drives Atlantic hurricane seasons and (1) rainfall amounts in the wintering grounds, (2) winds across migration corridors, and/or (3) other environmental responses that impact birds' survival.

Knowing whether migrating birds are being killed or displaced by storms and/or other meteorological and climatic teleconnection patterns is especially important today in the face of further declines in North American bird abundance brought on by the expanding human footprint, rapid climate change, and more extreme weather events. An in-depth understanding of the impact of cyclones and/or related oceanic-atmospheric structures on bird migration could provide valuable insight into new subdisciplines and studies in aeroecology and meteorology.

Introduction

Birds' annual migrations represent some of the most spectacular movements of animals on our planet, with enormous numbers of individuals moving hundreds, thousands, and even tens of thousands of kilometers annually. Birds that migrate annually between their breeding grounds in the North American temperate latitudes and the Neotropical wintering grounds in the Caribbean, South and Central America (Hayes, 1995) number in the billions (Dokter et al., 2018). This Nearctic-Neotropical system evolved as the North American climate changed over the past 65 million years. What was once a continent-wide belt of relatively mild and moist conditions gradually differentiated into a patchwork of tundra, woodland, grassland and deserts with more extreme temperature and precipitation regimes. Birds started to migrate seeking gentler climates, better resource availability, and less competition or predation (Cox, 1985). The present-day temperate and tropical latitudes in the geographical range of the bird migrants experience intra- and inter-annual meteorological variability that is sometimes driven by short- and long-term coupled ocean-atmosphere climatic variations.

Avian habitats, migratory corridors, and resting and refueling stops can all be impacted by the weather. As first summarized by Richardson (1978), winds are a particularly important factor influencing bird flight behavior (e.g., Drymon, et al., 2019; Horton, Van Doren, Stepanian, Farnsworth, et al., 2016; Horton, Van Doren, Stepanian, Hochachka, et al., 2016; Horton et al., 2018; La Sorte et al., 2015; La Sorte et al., 2018; Newton, 2007). For example, birds returning from the Neotropics in spring that encounter strong headwinds or crosswinds must stop more frequently to refuel – and when encountering extreme conditions in addition to headwinds, such as heavy rain, these stopping events may be dramatic, known as 'fallouts' (Clipp et al., 2020; Moore and Kerlinger, 1987; Tracey and Greenlaw, 2011). Although migrating birds possess an impressive set of weather-sensing skills, including abilities to assess changes in wind (Bingman and Moore, 2017; Wiedner et al., 1992), visibility and moisture in the air (A. Farnsworth, personal communication, December 10, 2020), as well as barometric pressure (Metcalfe et al., 2013), birds may not always avoid negative impacts of unfavorable and severe weather (Newton, 2007), particularly when they must travel over water (Diehl et al., 2014; Drymon et al., 2019).

Specifically, tropical cyclones (TC) have been known to displace or kill birds – an outcome often termed a bird ‘wreck’. The most common Atlantic TC paths cross all or portions of all the Nearctic-Neotropical migrant bird flyways (Figure 1). In his book *A Furious Sky: The Five-Hundred-Year History of America’s Hurricanes* (2020), Eric Jay Dolin relays historical accounts of birds impacted and displaced by hurricanes. South of Cuba in October 1780, the British Royal Navy’s HMS Phoenix braced for a storm that was rapidly closing in after having leveled Jamaica. First Lieutenant Benjamin Archer noticed birds “dropping out of the sky and diving toward the deck, where many of them were knocked unconscious” (Dolin, 2020). In the Great September Gale of 1815 which hit Long Island and New England, lexicographer Noah Webster noted how sea spray in Massachusetts had been transported far inland along with seagulls, “some of which were blown all the way to Worcester, about 45 miles from the ocean” (Dolin, 2020). Closer to the present day, between 1960 and 1985 a strong positive correlation was found between the number of wrecked Sooty terns (*Onychoprion fuscatus*) and both the amount and intensity of tropical cyclones (Huang, Bass Jr & Pimm, 2017). In 2005’s Hurricane Wilma, thousands of Chimney swifts (*Chaetura pelagica*) were killed or displaced thousands of kilometers, leading to a significant decline in the breeding population (Dionne et al., 2008). Radar and ground observations showed Hurricane Irene in 2011 displacing birds with tropical ranges as far north as New York (Van Den Broeke, 2013). In the first-ever recorded South

Atlantic hurricane on record, Atlantic petrels (*Pterodroma incerta*) were displaced and killed by the hundreds (Bugoni, Sander & Costa, 2007). And in a seminal study, Robert W. Butler (2000) found a significantly negative correlation between the abundance of two North American songbirds and the number of days with tropical storms in the Atlantic and Gulf of Mexico (GoM) during the preceding year's autumn migration between 15 August and 15 October.

Short-term climatic variations, most notably El Niño / Southern Oscillation (ENSO), can modulate the frequency and intensity of TCs in the Atlantic basin. The El Niño phenomenon tends to suppress Atlantic TC activity while La Niña enhances it (Gray, 1984; Klotzbach et al., 2017; Klotzbach et al., 2019). But El Niño (La Niña) can also strengthen (weaken) the trade winds across bird migrant corridors in the Caribbean and the Intra-Americas Sea (Amador, 2008), as well as suppress (enhance) precipitation in bird habitats (Grimm and Tedeschi, 2009; Ropelewski and Halpert, 1989; Tourigny and Jones, 2009). For example, increased rains from El Niño can alter vegetation characteristics in Swainson's Thrush (*Catharus ustulatus*) breeding grounds in California as well as their migration corridor of western Mexico and the Pacific coast of Central America, boosting demographic rates (LaManna et al., 2012). In contrast, Black-throated Blue Warblers (*Setophaga caerulescens*) are negatively impacted because they overwinter in the Caribbean and South America, where the El Niño can produce drought (Sillett et al., 2000). Drier environments produced by El Niño in South America can also impact migrant birds' energetic condition, causing them to stop at the first opportunity they get when flying northbound after crossing the GoM (Paxton et al., 2014).

Migrating birds fly mostly at night (Chapman, 1888; Lowery and Newman, 1966; Newton, 2010), taking flight as civil twilight turns to dusk generally 30 to 45 minutes after sunset (Hebrard, 1971). This attribute has posed significant challenges for direct study (e.g., visual) of the extent, magnitude, composition and ecology of their movements. Specific information about individuals can be attained through individual tracking data collected with ground-based biotelemetry and cellular phone networks, as well as from space with satellite-based sensors (Bridge et al., 2011; Seegar et al., 1996). Remote sensing techniques, among them ground-based thermal imaging and audio monitoring, allow scientists to track orders of magnitude more individuals (Horton, Shriver & Buler, 2015). The use of these remote sensing tools provides an opportunity for ecologists to study birds' foraging and migration behaviors, particularly those that occur under the cover of darkness. Among remote sensors, weather surveillance radar (WSR) has one of the longest avian legacies. During World War II, both Allied and German radars detected what at first were described as spurious echoes but soon were interpreted to be birds (Buss, 1946; Lack & Varley, 1945).

Modern radar systems have advanced significantly from the earliest versions designed to track aircraft. Today, polarimetric capabilities augment WSR's detection and depiction of precipitation patterns. Polarimetric radars transmit electromagnetic pulses both in a vertical and a horizontal orientation, allowing for better assessments of the variety, size and shape of the targets being remotely sensed (Kumjian, 2013). Improved algorithms can determine the type of precipitation being detected and – through the application of the Doppler effect – its movement in relation to the radar station. These techniques have resulted in a slew of radar-derived products that expand meteorologists' abilities for live monitoring of the dynamics of potentially severe weather, including winds aloft, rotating thunderstorms that can be precursors to tornadoes, hail shaft formation, and tornado debris signatures (Kumjiam, 2018). Extensive WSR networks designed to constantly monitor for these potentially threatening phenomena now exist in the United States and Europe.

While the characteristics of radar signal returns from biological targets are much different than those of precipitation (Gauthreaux and Diehl, 2020), the now-vast WSR arrays provide ample opportunity to study fauna in flight. WSR data are routinely "contaminated" – from a meteorologist's point of view – by insects (Ainslie & Jackson, 2011; Melnikov, Istok, & Westbrook, 2015; Mueller & Larking, 1985), bats (Gurbuz et al., 2015; Stepanian et al., 2016), and birds (Kelly and Horton, 2016). Methods to classify radar returns as biological instead of meteorological have been maturing since the 1960s (Gauthreaux, 1996) and have significantly improved in the past decade after the deployment of polarimetric radars (Kilamby et al., 2018; Melnikov et al., 2015; Stepanian, et al., 2016; Zrnić and Ryzhkov, 1998).

The emerging science of aeroecology has found immense utility in the expanding suite of WSR-derived products and applied them to better understand how flying organisms forage and migrate. Aeroecology is interdisciplinary and includes experts in atmospheric and earth science, geography, biology, computer science and engineering, among other disciplines (Kunz et al., 2007). In the last few years, ornithologists and aeroecologists have been perfecting radar signal processing methods to study avian ecology – producing bird count estimates (Gauthreaux and Belser, 2003), examining triggers (Horton et al., 2020) and patterns of migration (LaSorte et al., 2018), flight trajectories over commonly used flyways (Gauthreaux et al., 2006), and locating stopover and roosting sites (Gauthreaux and Belser, 1998). The remote sensing algorithms have reached a level of sophistication that today allow for the development of impressive bird migration visualization and forecasting tools (Shamoun-Baranes et al., 2016; Van Doren & Horton, 2018).

The GoM region is one of the busiest bird migration corridors in the Western Hemisphere. More than half of the North American species that winter in the tropics must negotiate the GoM by flying over or around it twice yearly (Lafleur et al., 2016). Analysis of radar imagery has revealed that approximately 4 billion migratory birds are estimated to pass through there each year (Dokter et al., 2018; Horton et al., 2019). Dokter et al. (2018) also found that of the total bird biomass migrating to the Neotropics in the fall, an estimated 76% returned in spring – a net loss attributed to mortality during migration and the overwintering period. Despite the fact that Neotropical migrants migrate longer distances, their overwinter survival was higher than for birds wintering in the temperate United States. These longer-distance migrants may rely on higher survivorship instead of a higher-recruitment strategy (Dokter et al., 2018). Even a small increase in deaths among birds that winter south of the United States could lead to significant population declines.

Knowing whether Nearctic-Neotropical bird migrants are being killed or displaced by Atlantic-basin hurricanes is particularly salient today. Findings from Rosenberg et al. (2019) indicate that the North American avifauna has decreased by nearly 30% in the last half-century – a staggering loss of nearly 3 billion birds. With climate change causing a greater proportion of tropical cyclones to become very intense (Knutson et al., 2020), North American bird populations could face further declines. A more holistic understanding of the causes for mortality at large spatiotemporal scales throughout the annual avian life cycle could improve bird population models (Loss et al., 2015), giving us a chance to formulate strategies to reverse the present trends. This research could contribute to our knowledge of overall bird mortality and further highlight the urgent need for conservation efforts across the Americas.

While a handful of past studies have shown that Atlantic tropical cyclones can negatively impact the populations of some migrant bird species, there has been no comprehensive measure of the effect of tropical cyclone activity on regional or large-scale changes in migration intensity.

A negative correlation between the number of migrating birds over or near the GoM in spring and the frequency and intensity of active hurricanes in the preceding late summer and fall might suggest a relationship between direct storm mortality and bird numbers. Alternatively, short-term climatic variability teleconnection patterns that drive Atlantic hurricane season activity also affect rainfall amounts in the wintering grounds and winds across migration flyways, which in turn may impact overall migrant fitness or survival.

Here, I studied the influence of tropical cyclone activity on Nearctic-Neotropical bird migrants. This research applied emerging techniques in radar signal processing to compare the number of migrating birds in fall to those returning in spring through common migration corridors near and over the GoM and parts of the U.S. Atlantic coast. The null hypothesis (H_0) was that the number of birds returning from the Neotropics in spring, as quantified by weather radars, was unaffected by tropical cyclone activity during the previous fall. The alternate hypothesis (H_A) was that very active hurricane seasons could cause a significant reduction in the number of Neotropical migrants that returned the following springs. To investigate direct links between storm mortality and migrant bird passage fluctuations, I also hypothesized that the relationship between storm activity and spring Gulf migratory passage would be stronger for regions that served as major migration corridors (e.g., GoM and Caribbean) than for areas with less migratory passage (e.g., the open Atlantic Ocean).

Data and Methods

Weather surveillance radar (WSR)

To quantify the intensity of bird migrations, I used unfiltered U.S. National Weather Service (NWS) radar data from 1995 to 2018, corresponding to nine WSR-88D NEXRAD stations spanning the longitudinal breadth of the GoM. The stations listed alphabetically and shown in Figure 2 were Biloxi MS (KLIX), Corpus Christi TX (KCRP), Elgin Air Force Base FL (KEVX), Houston TX (KHGX), Lake Charles LA (KLCH), Miami FL (KAMX), Mobile AL (KMOB), Tampa FL (KTBW) and Tallahassee FL (KTLH). These data are available from the National Oceanic and Atmospheric Administration's National Center for Environmental Information (NOAA/NCEI) via the Amazon Web Service portal (https://s3.amazonaws.com/noaa-nexrad-level2/index.html). While radars located at Key West FL (KBYX) and Brownsville TX (KBRO) are also on the coast of the GoM, I excluded these WSR stations from the analysis because they each are located approximately on the same longitude and in relative proximity to KTBW and KCRP, respectively. This minimizes the possibility of double counting migrants (i.e., counting the same bird on two different radars).

I used this 24-year dataset to estimate the intensity of spring bird migration across and near the GoM from 1 March to 15 June as well as the preceding fall migration from 1 August to 15 November. I examined samples taken every 30 minutes from 2,115 spring nights and 2,152 autumn nights from civil dusk to civil dawn – defined as the time the geometric center of the Sun is six degrees or more below the horizon. These WSR avian data sampling and extraction techniques follow Horton et al. (2020) and are summarized here.

Prior to examining the radar imagery to quantify migration activity, the WSR data were filtered for clutter and precipitation. Ground clutter came from buildings, wind turbines, communications antennas, and other stationary objects scanned by each radar's signal. Precipitation posed a different challenge. Legacy (i.e., non-polarimetric) WSR-88D data date back to the mid 1990s, when the radars were first deployed. Historically, these data had been difficult for aeroecologists to analyze because they lacked the polarimetrically derived products that facilitate object classification. Therefore, each legacy radar image required screening for possible precipitation or other unwanted echoes not relevant to bird monitoring. This process required human interpretation, a limiting factor for large-scale biological research with WSR-88D data. Fortunately, accelerating progress in computational capability and artificial intelligence led to the development of deep convolutional neural networks that separate biological returns from precipitation and background clutter (Lin et al., 2019).

The latter part of the radar time series benefited from an upgrade to polarimetric capability across the NWS WSR network. Completed in 2013, the upgrade for all 143 sampling locations of the NEXRAD network added new radar-derived products which, in addition to providing meteorologists with crucial information about weather phenomena (Zrnic et al., 2014), made it easier to distinguish between biological and precipitation signal returns (Stepanian et al., 2016). MistNet (Lin et al., 2019) is an aeroecology machine-learning method that can quantify avian biomass in WSRs. Polarimetric radar scans containing precipitation were used to train the MistNet algorithm, which can identify at least 95.9% of all biomass with a false discovery rate of 1.3%. Since the machine-learning process is fully automated, hundreds of millions of radar scans across any part of the WSR network can be processed, including those dating back 25 years.

Migration intensity was determined from radar reflectivity and bird migrant flight speed and direction – meaning that in spring the targets must have had a northward movement vector, versus a southbound component in autumn. Target speed, as measured by the radar's Doppler capability, allows for insects to be filtered out because they move much more slowly than birds (Stepanian, et al., 2016). For each NEXRAD station, nightly passage of migrants was then estimated by integrating the volume of avian targets over the sampling area through the night and using a generalized additive model to estimate total seasonal passage, following Horton et al. (2020). For a given radar, only years with more than 75% of nights present were used.

Atlantic tropical cyclone activity

To evaluate the level of TC activity during each late summer / early autumn bird-migration season, I used the Accumulated Cyclone Energy (ACE) index (Saunders, Klotzbach and Lea, 2017). At a single moment in time, ACE is equal to the square of the maximum TC sustained wind speed in knots, then divided by 10,000. The index for the full Atlantic basin for any day, month, or season is based on the sum of this calculation at 6-hourly intervals for all TCs in a basin (Yu and Chiu, 2012). While the ACE index is often calculated for the whole Atlantic basin over an entire year, it can also be measured for smaller geographic regions like the GoM, or for any timescale (P. Klotzbach, personal communication, December 10, 2020), such as the period of peak fall bird migration. ACE is highly dependent on TC count, TC longevity and maximum windspeeds and does not incorporate any of the other TC impacts like rain, waves, or storm surge. However, in my dataset, ACE was strongly correlated ($r = 0.9$) with Named Storm Days, another measure that does indirectly incorporate these additional TC impacts. Therefore, ACE was a useful index that captured variation across a range of possible TC impacts.

Analysis methods

I modeled bird passage with generalized additive mixed-effects models (GAM) (Hastie and Tibshirani, 1987) in R. I implemented a log-transformation to remove the skewness of the original data and facilitate the interpretation of model results as biologically informative proportional effects. I used two response variables: (1) log-transformed summed reflectivity factor for spring passage at each radar station (roughly proportional to the number of birds), and

(2) the ratio of log-transformed summed reflectivity factor in spring to the same metric calculated for the previous fall. The spring-to-fall migrant passage ratio provided a second way to test H_A independent of any yearly trends in total bird count.

I modeled spring passage as a function of whole Atlantic basin ACE for August to November, the peak of the fall migration season. When seeking correlations between many observations of the same subject – like migrating birds – which can experience random distortions from multiple sources of variability, and investigating manifold structures of correlation, linear mixed-effect modeling is a powerful tool (Oberg and Mahoney, 2007). I used the following predictor variables: year (GAM smoothed term), log-transformed sum of previous fall passage, ACE for the whole Atlantic basin, and radar identity (random effect; accounts for difference in average passage among radars). I included only years with at least three radars present (each with >75% data for that year). I quantified the influence of ACE in interpretable form by looking at the predicted difference in bird numbers between the 90th and 10th percentile ACE values.

Migration passage before 2005 was generally lower than after 2005. The NWS Radar Operations Center changed radar signal ground clutter filtering algorithms in the mid-aughts, and this change may have artificially boosted the radar reflectivity factor – proportional to bird counts – beginning around 2005 (Ice et al., 2007; Ice et al., 2009). I accounted for this overall trend by specifying year as a nonlinear predictor in the model. The spring-fall passage ratio did not show any long-term trend. Finally, I reran all models on only post-2005 data to ensure that the inclusion of pre-2005 data did not influence the result.

I then went on to compare different regions – the GoM, the Caribbean Sea, the open Atlantic west of sixty degrees west longitude (60°W), and the open Atlantic east of 60°W, north of the equator and west of the 0° meridian (Figure 3). I produced shapefiles in ArcGIS Pro for each of these regions, which then allowed for ACE values at 3-hour intervals to be extracted from NCEI. As above, I used linear mixed-effects models with the log-transformed sum of spring passage as the response variable, and included predictors for year (smooth), the log-transformed sum of previous fall passage, and radar ID (random effect). I compared the four models (one for each region) using Akaike Information Criterion corrected for small sample sizes (AIC_C), which is an estimator of prediction error and a way to assess the quality of statistical models relative to each other for a given set of data.

I repeated all the above analyses with the spring to fall ratio of the number of birds.

Results

Spring and Ratio of Spring to Fall

I found a highly significant negative relationship between ACE (summarized across the whole Atlantic basin from August to November) and spring bird passage, after accounting for long-term trends and the size of the previous fall's migration (Table 1; Figure 4). The predicted proportional change in migration traffic between full-year full-Atlantic ACE at the 90th percentile (ACE = 213) compared to the 10th percentile (ACE = 30) was 0.782. This represents a predicted decrease of 21.8% in the number of birds crossing the GoM area during springs following the most active Atlantic hurricane seasons compared to the least active seasons. This association is still strong when subsetting only to data after 2005 (a predicted decrease of 20.5%). Similarly, there was a 17.1% predicted decrease in the ratio of spring passage to fall passage between ACE = 213 (90th percentile) and ACE = 30 (10th percentile) – a predicted proportional change of 0.829 (Table 2; Figure 4).

Regional Comparisons

Spring Passage

The eastern North Atlantic's August to November TC activity (ACE) was the best predictor for spring passage (Table 3). The whole Atlantic's TC activity in the same period followed closely. Together, basin and North Atlantic measures had a total AIC weight of 0.966. Conversely, ACE measures in the Caribbean Sea and GoM had little support, receiving a combined AIC weight of only 0.034. For these regions, the association between ACE and migration traffic was not statistically significant.

Fall

In fall, whole-basin August to November ACE was not a significant predictor (Table 4; Figure 4; $p = 0.848$).

Discussion

Migrating (and migratory) birds face an increasing array of challenges, and the multi-fold impacts from rapidly changing climate have potential long ranging consequences. One of these challenges is the possibility of birds encountering limiting factors across non-breeding grounds as modulated by regional precipitation accumulations that are potentially trending drier in the long term due to climate change (La Sorte et al., 2017; Imbach et al., 2018; Taylor et al., 2018). The rapidly changing climate is also supercharging one of the more sizeable threats to migrating birds: The proportion of named tropical storms reaching high to extreme intensities and classified as Category 3, 4 and 5 cyclones globally is on an upward trend (Knutson et al., 2020) which is expected to continue (Knutson et al., 2010). While the North Atlantic Ocean has seen an uptick in the frequency of TCs in recent decades, including a record thirty named tropical storms in 2020, no such trend is observable globally (Murakami et al., 2020) and climate models generally project a decrease in the global frequency of TCs (Yoshida et al., 2017). But it is the intense TCs that produce the biggest impacts (Winkle et al., 2020), and birds today face a higher risk of running into extreme weather produced by increasingly intense hurricanes. Studying the variations brought on by the changing climate, particular extremes such as the increasing intensity of cyclones, has great value in the context of avifauna given the recent decline of North American bird populations.

This is the first integral view of the effects TCs on bird migration intensity. Salient past studies on the impacts of TCs on birds had looked at a handful of individual species, but not at the breadth of Neotropical migrants across the width of the GoM. Additionally, this study is based on a quarter-century of WSR data which includes legacy imagery from the non-polarimetric NEXRAD network when it was first deployed in the mid 1990s. Analysis of avian targets across the full period of record of WSR data would have been impractical if not impossible just a few years back before the development of deep convolutional neural networks like MistNet that can separate biological returns from precipitation and background clutter.

The highly significant negative relationship between whole-Atlantic TC activity and migrant bird GoM passage during the subsequent spring supported the alternate hypothesis (H_A) that very active hurricane seasons are associated with a reduction in the number of Neotropical migrants that return the following spring. The relationship was strongly negative regardless of whether I looked at shorter-term trends or the ratio of spring to fall bird passage, an important added test for the H_A that removed any impact from changing year-to-year migrant population trends. When Atlantic hurricane seasons were very active (i.e. 90^{th} percentile of activity), bird passage over and near the GoM during the following spring was approximately 20 percent lower than following seasons when there was very low TC activity (10^{th} percentile of activity). In contrast, fall bird passage was not well predicted by August to November ACE.

Another way to exemplify these findings is by examining individual hurricane seasons and the migrant traffic that followed in spring. 1995 was the first year in which the Atlantic Multidecadal Oscillation (AMO) flipped to positive after decades in which the index had been negative. The AMO, which is driven by the speed of the Atlantic Meridional Overturning Circulation (AMOC) ocean current, manifests as long-duration changes in the sea surface temperature (SST) of the North Atlantic Ocean, with cool and warm phases typically each lasting 20 to 40 years. The positive or warm AMO phase and the resulting hotter-than-normal water temperatures generally produce more active Atlantic hurricane seasons, modulated most often by ENSO (Alexander et al., 2014; Knight et al., 2006). The 1990s had started off with generally inactive hurricane seasons. Annual Atlantic-wide ACE averaged only 46 from 1991 to 1994 despite 1992's infamous Category 5 Hurricane Andrew. Then came the 1995 season in which 19 tropical storms formed out of which 11 reached hurricane strength. Impactful Major Hurricanes Luis and Marylin struck the Caribbean while Opal and Roxanne hit the GoM. The Atlantic-wide ACE for the 1995 season was 227. For the following spring, the return migration across the GoM was calculated to be the third lowest in the radar time series. The only two springs with lower migrant traffic were 1999 and 2000, which also followed very high seasonal ACE index values of 181 and 177 for 1998 and 1999 respectively. Conversely, the ratio of spring 2014 to fall 2013 bird passage over the GoM was ranked second highest in the timeseries. Despite a generally hyperactive period from 1995 to 2012 in which ACE averaged 140, a remarkably inactive 2013 yielded an ACE of only 36. Only two hurricanes formed that year, none major, and only one – Ingrid – impacted the GoM region.

While the strong negative correlation between whole-Atlantic fall ACE and spring GoM passage might imply that storms directly impacted or even wrecked birds, my additional findings confound that premise. Paradoxically, the relationship between Gulf migratory passage and storm activity in the GoM and the Caribbean is weak, despite their status as major bird migration corridors. On the contrary, ACE measured over the open North Atlantic Ocean was tightly associated with migratory passage, even though far fewer birds migrate over this region. This contrast does not support a direct link between storm mortality and observed passage fluctuations.

It is worth repeating that the ACE index is highly driven by maximum TC windspeeds. TC impacts other than storm winds may be wrecking spring migrants. Although birds generally try to avoid flying in precipitation (e.g., Van Den Broeke and Gunkel, 2020), birds migrating over open water are forced to continue flying, which may lead to increased mortality (e.g., Richardson, 1978). An alternate measure of TC activity that incorporates rain (by proxy) but does not overweigh windspeed is "Named Storm Days". A TC's maximum sustained winds must reach 35 knots (18 m/s) before it is named and classified as a tropical or subtropical storm. Therefore, named storms include TCs that have exceeded tropical depression strength, up to and including major hurricanes. Precipitation can often be of extreme intensity even in systems well below hurricane strength that do not produce much ACE. However, my analysis of ACE versus Named Storm Days as a predictor for spring bird passage showed that the two measures were highly correlated ($r = 0.9$). Hence, Named Storm Days yield essentially the same findings – spring migration across the busiest GoM and Caribbean corridors is not significantly correlated to the preceding fall's TC activity in those areas. These questions about causality point to the likelihood that it is a combination of factors causing bird losses, only one of them possibly being direct storm impacts – though not even that is clear from these results.

A teleconnection is a causal connection or correlation between short-term climatic patterns and meteorological or environmental conditions elsewhere. Some of these coupled ocean-atmosphere climatic variations can modulate Atlantic hurricane season activity. The teleconnection between ENSO and Atlantic hurricane activity is well understood. ENSO teleconnections also impact rainfall accumulation in Neotropical bird wintering grounds and winds across migration flyways. These environmental conditions in turn can impact overall bird migrant fitness or survival. While the characteristic decrease in Atlantic TC activity during an El Niño might mean less fall migrant entanglements with stormy weather, the birds could also encounter drier wintering grounds with a reduced carrying capacity when El Niño is occurring.

The Atlantic Meridional Mode (AMM) is a non-ENSO interannual climatic oscillation characterized by an anomalous SST gradient between the Atlantic and Pacific tropical oceans (Chiang and Vimont, 2004). When this SST-based index is lower or negative, trade winds are stronger and SSTs in the TC Main Development Region (MDR) of the tropical Atlantic are colder. These conditions can temporarily shift TC genesis regions away from the MDR (where most of the strongest hurricanes normally originate) and suppress Atlantic TC activity overall (Kossin and Vimont, 2007). ENSO and AMM vary independently from each other.

Because birds can be affected by one or more of these and other short-term climatic oscillations and their resulting teleconnections (droughts, winds, storms) it is difficult to measure the relative impact of each meteorological pattern on the migrants – much less the combined net effect when many of them occur at once. Some are favorable and others unfavorable for birds.

The full spectrum of variables impacting Neotropical bird migrants has yet to be revealed. Other teleconnections that might impact bird migrations like the North Atlantic Oscillation (NAO), to name one, are worthy of investigation. Regardless of the underlying mechanisms, my finding that whole-Atlantic hurricane activity in the late summer and fall negatively impacts the number of Neotropical migrants returning across and near the GoM in spring stands as a first step which will hopefully launch further investigations. The methods employed in this research can be readily replicated, which will allow for a statistically robust dataset that can encompass at minimum 30 years – something not possible until 2025.

Beyond problems posed by the expanding human footprint, birds are facing increasing challenges from an anthropogenically changing climate. For the Neotropical long-distance migrants that rely on higher survivorship (Dokter et al., 2018), any increase in mortality can have important long-term implications on populations. Continuing research into the interlinkages of weather, climate and birds can be invaluable as fodder for understanding proximate and ultimate behaviors as well as the mechanics of the systems. As we build towards aggregate knowledge, this prospective new subdiscipline of aeroecology could result in improved conservation strategies being cast to steady or reverse the present trends in avian populations.

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Tables

Table 1. Linear mixed-effect model for accumulated cyclone energy (ACE) and spring bird migration traffic, accounting for long-term trends. The response variable is spring migratory bird passage, and ACE is summarized across the whole Atlantic basin from August to November.

Fixed effects

Term	Estimate	Std. Error	t value	P-value
(Intercept)	15.6	0.291	53.4	<0.001
Fall migration passage (log-transformed, scaled)	0.313	0.0564	5.55	<0.001
ACE (whole Atlantic basin)	-0.00134	0.000442	-3.04	0.003

Smooth and random effects

Term	edf	Ref.df	F	P-value
Year (smooth)	5.23	6.31	2.71	0.015
Radar (random)	7.95	8	196	<0.001

Table 2. Linear mixed-effect model for accumulated cyclone energy (ACE) and spring bird migration traffic, accounting for long-term trends. The response variable is the ratio of spring to fall migratory bird passage, and ACE is summarized across the whole Atlantic basin from August to November.

Fixed effects

Term	**Estimate**	**Std. Error**	**t value**	**P-value**
(Intercept)	-0.891	0.325	-2.74	0.007
ACE (whole Atlantic basin)	-0.00103	0.000414	-2.48	0.014

Smooth and random effects

Term	**edf**	**Ref.df**	**F**	**P-value**
Year (smooth)	1	1	0.406	0.525
Radar (random)	7.95	8	147	<0.001

Table 3. Regional comparison of ACE models. Comparison of four regional models and the whole basin model using Akaike Information Criterion corrected for small sample sizes (AICc).

	ACE slope	ACE P-value	logLik	AICc	delta	weight
N Atl East	-0.0024	0.0089	-19.5	67.4	0.000	0.4520
Whole basin	-0.0011	0.0115	-19.8	67.9	0.501	0.3520
N Atl West	-0.0024	0.0266	-20.6	69.5	2.050	0.1620
Caribbean	-0.0017	0.2360	-22.5	73.3	5.890	0.0237
Gulf	0.0001	0.9720	-23.2	74.8	7.400	0.0112

Table 4. Linear mixed-effect model for accumulated cyclone energy (ACE) and fall bird migration traffic, accounting for long-term trends. The response variable is fall migratory bird passage, and ACE is summarized across the whole Atlantic basin from August to November.

Fixed effects

Term	**Estimate**	**Std. Error**	**t value**	**P-value**
(Intercept)	16.5	0.157	105	<0.001
ACE (whole Atlantic basin)	8.71e-05	0.000455	0.191	0.848

Smooth and random effects

Term	**edf**	**Ref.df**	**F**	**P-value**
Year (smooth)	5.22	6.31	5.39	<0.001
Radar (random)	7.84	8	44.6	<0.001

Figures

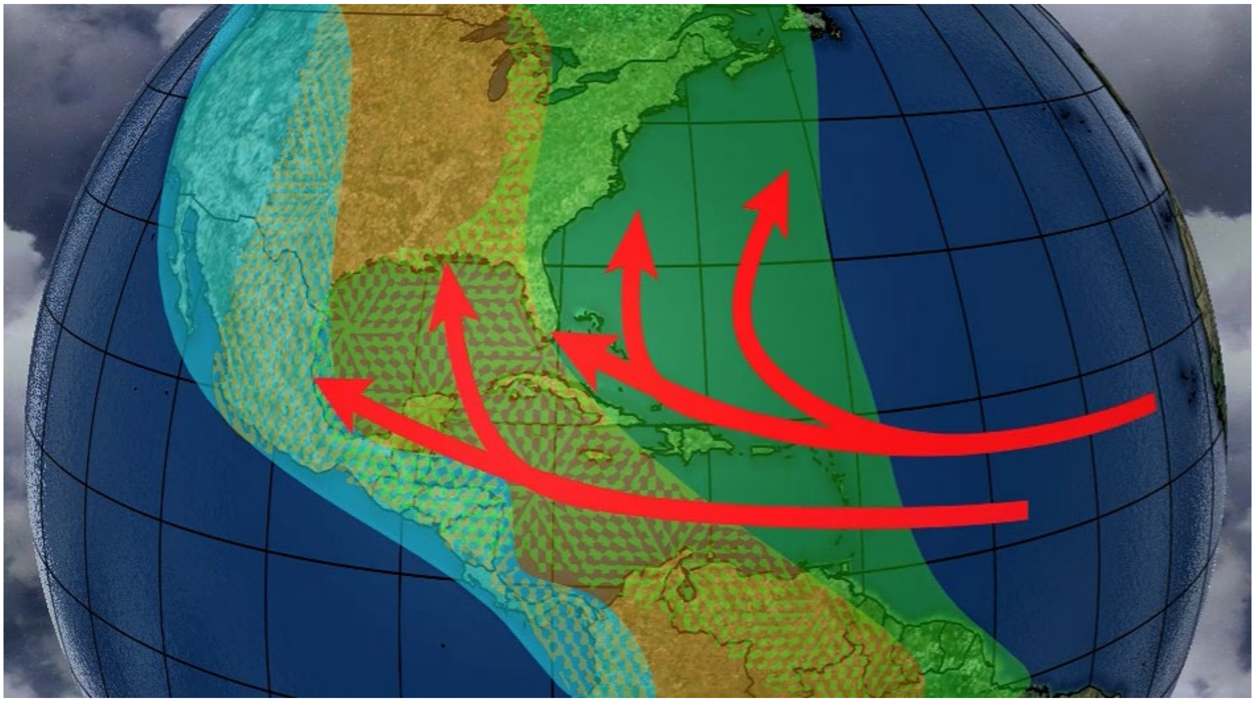

Figure 1. Bird migration routes and typical tracks of Atlantic tropical cyclones. Frequent tropical cyclone paths (red, from National Hurricane Center, www.nhc.gov/climo) superimposed on broadly defined Nearctic-Neotropical migration routes (from BirdLife International). Birds may interact with storms in the Americas' Atlantic (green), Central (orange), and Pacific (blue) migration routes.

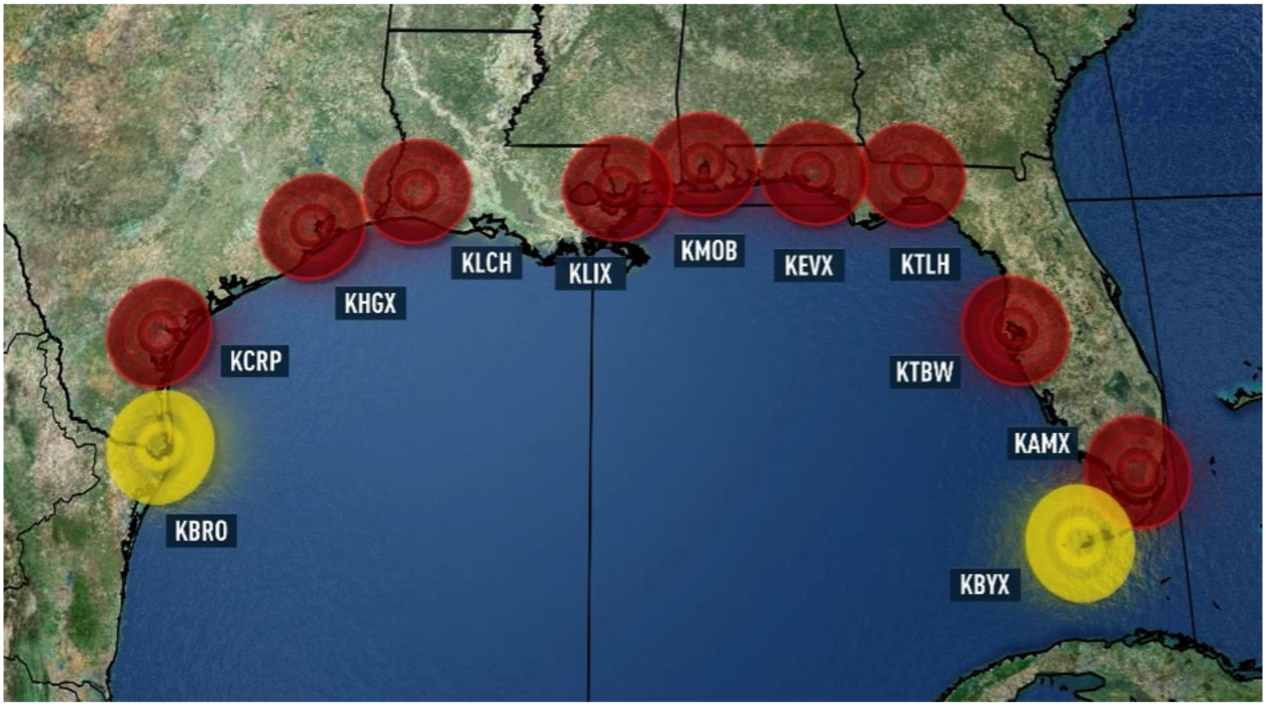

Figure 2. NEXRAD WSR stations along the Gulf of Mexico. Locations of weather surveillance radar (WSR-88D) stations in the immediate proximity of the Gulf of Mexico. Circles depict surveillance radii of 100 kilometers where the beam centers at an altitude of 1,500 meters and samples an area ~1,500 meters in diameter. The Brownsville TX (KBRO) and Key West FL (KBYX) radars are shown in yellow because their data were not used in the analysis.

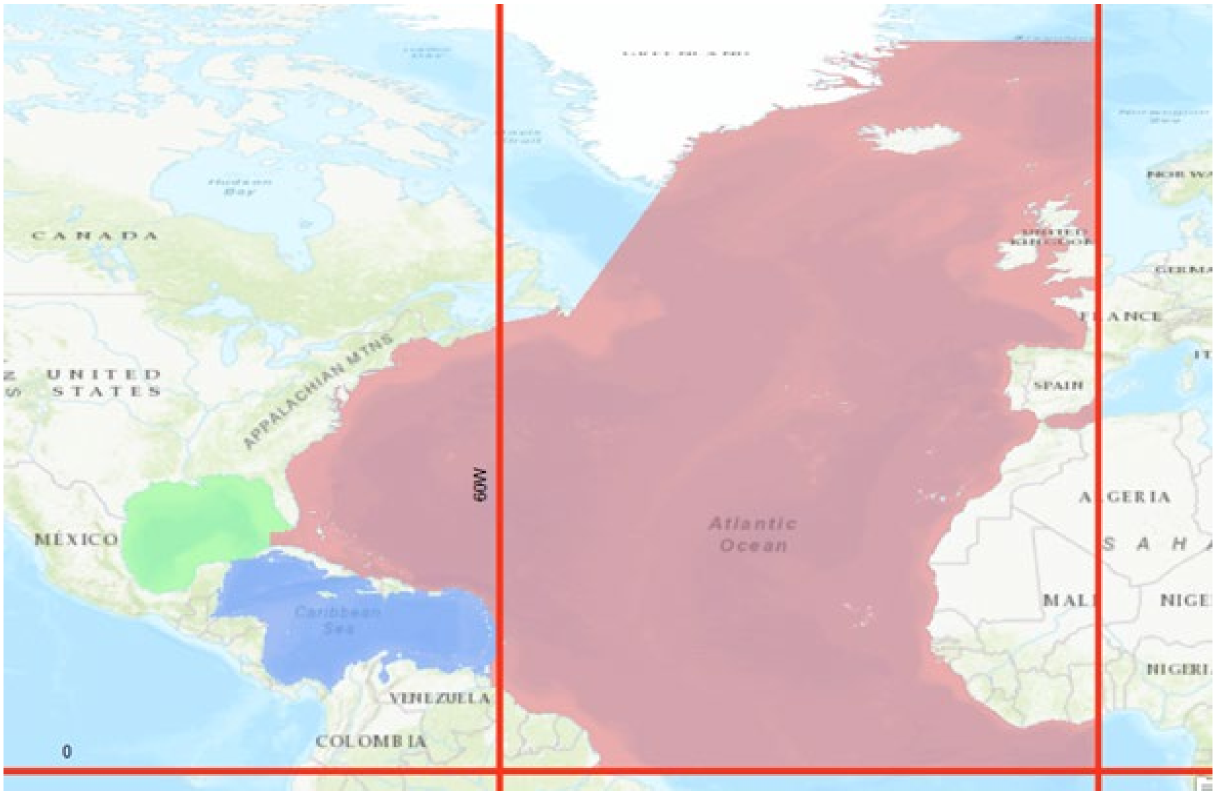

Figure 3. Geographic extent and characterization of accumulated cyclone energy (ACE). The four areas selected for regional investigation of ACE and Named Storm Days: The Gulf of Mexico, the Caribbean Sea, the open Atlantic west of 60°W, and the open Atlantic east of 60°W, north of the equator, and west of the 0° meridian. Shapefiles were produced in ArcGIS Pro for each of these regions.

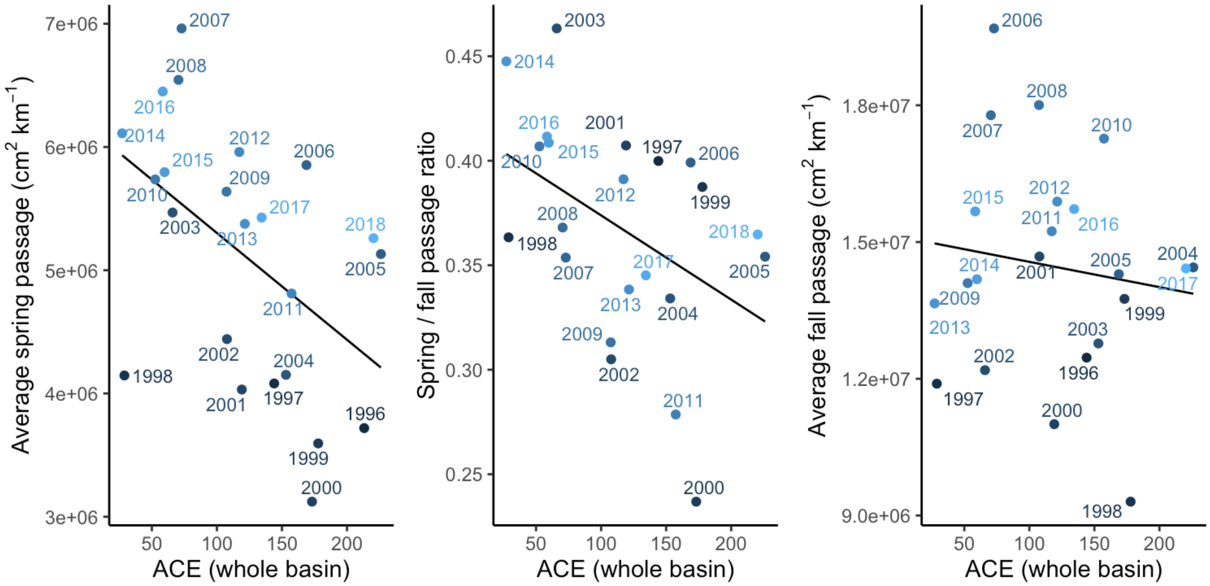

Figure 4. ACE versus bird migration passage through the Gulf of Mexico region. Whole-basin Atlantic Accumulated Cyclone Energy (ACE) from August to November 1995 to 2017 versus average passage across the GoM radars in the subsequent spring (left) and concurrent late summer and fall (right). The middle graph plots ACE measured in the same fall period versus the ratio of average spring to fall passage across the GoM radars.