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Timothy J. Gunkel

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The influence of isolated thunderstorms and the low-level wind field on nocturnally migrating birds in central North America

Matthew S. Van Den Broeke & Timothy J. Gunkel

Department of Earth and Atmospheric Sciences, University of Nebraska-Lincoln, 126 Bessey Hall, Lincoln Nebraska, 68588, USA

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convection, environment, migration, radar, thunderstorms

Abstract
Seasonal bird migration occurs on large spatial scales and is influenced by many factors including weather conditions. Weather can include thunderstorms, which may force migrants to land or cause them to reroute a migration path. In this study, a sample of isolated thunderstorms was analyzed from the domains of three weather radars in the central United States to test hypotheses regarding the influence of thunderstorms on the distribution of migrants. Migrating bird density was often reduced in the wake of storms, and this wake reduction was typically more pronounced for larger, more intense and faster-moving storms, particularly in eastern Nebraska. Wind conditions more strongly influence the distribution and density of migrating birds in fall than in spring, providing evidence that migrating birds respond to environmental signals more readily in the fall. This finding supports the concept that birds are more strongly obligated to cover distance in the spring and arrive in their breeding range on time. Wind conditions at the surface were generally more important to migrant density and distribution than wind conditions closer to flight level.

Introduction
Large-scale seasonal bird migration is a global phenomenon with large ecological and economic implications. Especially since migrating bird biomass has shown substantial recent decreases (e.g. Rosenberg et al. 2019), understanding factors which influence migration dynamics is critically important. Such factors range from continent-scale (e.g. land cover modification) to local-scale. Beyond anthropogenic impacts, natural influences such as weather may also play an important and variable role. In this paper, we begin to examine the influence of isolated thunderstorms and the low-level wind field on nocturnal bird migration.

Migration timing varies between species (e.g. Shamoun-Baranes et al. 2017). Most relevant to this study, after sunset boundary layer thermals disappear and atmospheric turbulence correspondingly decreases (e.g. Kellinger and Moore, 1989). Wind speed aloft may increase as turbulence weakens, manifesting as a nocturnal jet (e.g. Shamoun-Baranes et al. 2017). For example, a springtime southerly low-level jet often occurs over the central United States (Parish et al. 1988), potentially increasing migration efficiency (e.g. Wainwright et al. 2016). Springtime migration for many species is March through May, corresponding to the time when surface resources grow in abundance in northern latitudes (Költzsch et al. 2014; Streby et al. 2015; Nadal et al. 2018). Fall migrants return to their wintering locations; this equatorward flux of biomass generally peaks in intensity during September and October in eastern North America (e.g. Mills 2005; Van Buskirk et al. 2009).

In North America, migrating birds may follow loosely defined ‘flyways’ (e.g. Fourment et al. 2017). During migration, birds often rest at stopover locations to take advantage of local resources (e.g. Weber and Houston, 1997). Stopover locations in eastern North America often include areas with a large tree density, such as urban parks (e.g. Bonter et al. 2009; Buler and Dawson, 2014). Migrating water birds often stop at wetlands and lakes.
Convection Effects on Nocturnally-migrating Birds

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(e.g. Niemuth et al. 2006; O’Neal et al. 2012). Some migrating birds may use river valleys, including raptors (e.g. Bildstein et al. 2008) and waterfowl (e.g. Bellrose 1957; Bellrose 1968; Serie et al. 1983). Recent work, however, has questioned whether migrating waterfowl use river valleys for navigation as extensively as was thought prior (O’Neal et al. 2014). Although the use of landscape features during migration is less-known for passerines, it stands to reason that in eastern North America river valleys may be preferred because of their relatively higher tree density, especially in agricultural areas of the Great Plains and Great Lakes regions.

Meteorological conditions influence the navigation decisions and rerouting of migration (Berthold 2001; Both 2010; Vansteelandt et al. 2017; Eisaguirre et al. 2018). Eisaguirre et al. (2018) studied the effects of wind, clouds/precipitation and barometric pressure on the migration of eagles from Alaska to western North America, and found that the winds can be energy efficient when there is a tailwind, and inefficient when there is a headwind (e.g. Kemp et al. 2012). The potential effects of a large tornado-producing storm system on the movements of golden-winged warblers (Vermivora chrysoptera) during spring migration have been investigated by Streby et al. (2015) using light-level geolocators. It was hypothesized that infrasound associated with a storm system over the central Great Plains may have caused the warblers to reroute on their way to a nesting site or evacuate the site if they arrived early. Controversy regarding such application of light-level geolocator data has been discussed (Lisovski et al. 2018; Streby et al. 2018). Although there is still much to learn about biological detection and interpretation of infrasound, the results of Streby et al. (2015) indicate that it may provide information to migrants regarding nearby convection or the larger-scale weather systems which produce it. Migrants may not be able to avoid convection, potentially leading to large mortality (e.g. Diehl et al. 2014).

Large-scale migratory patterns in North America are reasonably well-known (e.g. Van Doren and Horton, 2018). Understanding smaller-scale influences on migratory behavior is considerably less developed. This paper focuses specifically on the effects of isolated nocturnal convection on migratory behavior in the domains of three central U.S. weather radars. We hypothesize that migrant density is reduced in the wake of and on the down-migration side of thunderstorms. We also seek to determine particular storm characteristics and/or low-level wind conditions that most influence navigation decisions of migrants near thunderstorms. It is hypothesized that these effects will increase as the size and intensity of the storms increase, assuming that migrants will seek to avoid hazards within convection (turbulence, heavy precipitation, hail). We also hypothesize that the background density of migrants is larger on days with a more favorable wind direction for migration, and that the effects of storms on the distribution of migrants is larger on days with a more favorable background wind field for migration. This study is the first to our knowledge to quantitatively address the effect of isolated thunderstorms on biomass density during migration, and may be used as a baseline to investigate the effects of larger-scale convective events on nights which are otherwise favorable for migration.

Methods

Nocturnal (sunset to sunrise) convective cases were analyzed. Nocturnal migration was considered since many bird species migrate at night and since insects typically do not fly at high altitudes during these hours (e.g. Chapman et al. 2011); thus the total biomass density is likely dominated by birds. This choice of analysis time may be prone to error if large numbers of nocturnally active insects were present as may sometimes occur, though this was not commonly observed in this study. Spring (April/May) and fall (September/October) were investigated since these are well-known migration times for many North American species (e.g. Van Buskirk et al. 2009; Kölsch et al. 2014; Streby et al. 2015). In spring, northward migration is assumed since many species follow increasing resources. In the fall, southward migration is assumed as resources grow scarce to the north.

Migration density can be monitored on large spatial scales using radar networks. In the United States, the Weather Surveillance Radar-1988 Doppler (WSR-88D) network has been used in ornithological studies for many years (e.g. Gauthreaux and Belser, 1998; Gauthreaux et al. 2003; Gauthreaux et al. 2008; Bonter et al. 2009; Buler and Dawson, 2014). Although base reflectivity factor \( Z_{HH} \) can indicate the presence of bioscatter (birds, insects, bats), it cannot be used for species-level identification without additional information such as ground truth (Gauthreaux et al. 2008). Polarimetric capability added to the WSR-88D network in 2012–2013 can increase confidence in the classification of an echo as biological (e.g. Van Den Broeke 2013). During spring and fall migration, a migration signature is often apparent in both \( Z_{HH} \) and radial velocity \( V_r \). Migrants generally move in the same direction and the detected \( V_r \) is close to their ground speed (Gauthreaux and Belser, 1998; Gauthreaux et al. 1998). Algorithms have been developed which utilize radar data to determine bioscatter density within a sample volume, allowing quantification if target identity is known (e.g. Vaughn 1985; Chilson et al. 2012; Van Den Broeke 2019). In this study, three WSR-88D sites were selected for analysis of migratory behavior with
respect to nocturnal convection because of their proximity to major rivers, which may provide stopover habitat for many species and/or serve as navigation guides during migration (e.g. Serie et al. 1983; Bildstein et al. 2008; Smith et al. 2012). These sites were Omaha, Nebraska (KOAX), which is near the Missouri, Platte and Elkhorn Rivers; Davenport, Iowa (KDVN), close to the Mississippi River; and Evansville, Indiana (KVWX), near the Ohio and Wabash Rivers.

Thunderstorm cases were drawn from 2013 to 2019, when dual-polarization was available on the WSR-88D network, and storms with varying size and intensity were included. Cases were limited to this temporal range so that cross-correlation coefficient ($\rho_{hv}$) could be used to increase confidence that a sampled area was dominated by biological scatter and that no precipitation was mixed in (e.g. Park et al. 2009; Van Den Broeke 2013). Cases had to be embedded within a clear migration signature (Fig. 1A), defined as a relatively uniform region of $Z_{HH}$ (generally 15–30 dBZ) fairly symmetrically surrounding the radar site and containing a clear $V_r$ signal indicating northward (southward) movement during spring (fall). The migration signature was also required to contain $\rho_{hv} < 0.80$, eliminating meteorological scatterers. Individual thunderstorms and storm clusters were required to be separated from other convection by at least 15 km and to persist as isolated cells for at least six consecutive radar sample volumes. All storms were within 100 km of the radar site to increase the quality of biomass density estimates, since the sample volume size increases with distance from a radar. Relatively few storms survived the imposition of these criteria (Appendix S1). The analysis period for each storm began when that storm first met the criteria described above and ended when it no longer did (most commonly, the storm moved outside the allowable range or outside the well-defined migration signature, or became too close to other convection to be considered isolated). Convective characteristics were analyzed for each selected storm. Specifically, the areal extent of 35-dBZ $Z_{HH}$ and the 90th percentile of the $Z_{HH}$ values were analyzed for each time step of each cell at base scan level. After these values were calculated for each time step, the storm average of these values was calculated for each case.

At each time step, four regions were defined around the storm of interest (Fig. 1A):

1. **Wake region**: the region extending 10 km away from the storm’s edge in the direction the storm was moving away from. This was the region over which the storm had recently tracked (region ‘1’ in Fig. 1A). It was hypothesized that migrant density is low in this area, since migrants may go to the surface to avoid hazards when a storm is overhead.

2. **Ahead region**: the region extending 10 km away from the storm in the opposite direction as the wake region (e.g. in the direction the storm was moving; region ‘2’ in Fig. 1A). This was hypothesized to generally represent the background migration signature, though it could be affected by storm proximity if migrants avoid approaching convection.
3 **Migrant approach region**: the region extending 10 km away from the storm in the direction from which migrants were approaching (region ‘3’ in Fig. 1A). The direction of migrant approach was defined as the large-scale migrant direction of travel at the same time, at approximately the same height as the migrant approach region. It was hypothesized that this side of the storm represents the background migrant density, or should possibly experience a slight increase in migrant density as migrants approached the storm and slowed down.

4 **Migrant away region**: the region extending 10 km away from the storm in the direction opposite the migrant approach region (e.g. in the direction toward which migrants were flying; region ‘4’ in Fig. 1A). This region represents an area that is ‘blocked’ by the storm, assuming that migrants do not fly through thunderstorms. It was hypothesized that migrant density within this region is relatively low.

Overlap was possible between these areas. For example, if a spring storm was moving toward the northeast, the wake and approach regions would likely overlap in the northeast direction from the storm.

Once the regions described above were manually defined, a biomass density value was calculated inside each. Biomass density was calculated following Chilson et al. (2012) and Van Den Broeke (2019). In summary, the $Z_{HH}$ value [dBZ] for each sample volume was converted to units of dB using:

$$\eta = Z + 10\log_{10} \left( \frac{1000\pi^2 K_m^2}{\lambda^4} \right), \quad (1)$$

where $\eta$ = reflectivity [dB], $Z$ = raw $Z_{HH}$ [dBZ], $K_m^2$ = the complex dielectric constant which is usually set to 0.93 assuming that biological scatterers are primarily liquid (e.g. Chilson et al. 2012), and $\lambda$ = the radar wavelength [cm]. Reflectivity [dB] was then converted to linear units:

$$\eta_{lin} \left[ cm^2 km^{-3} \right] = 10^{\eta/10}, \quad (2)$$

which relates the reflctivity measurement to a physical cross-section [cm$^2$] of scatterers in the sample volume. Linear reflectivity is then multiplied by volume of the sample [km$^2$] to yield total scatterer cross section [cm$^2$] in that pixel, using the standard equation:

$$Vol = \pi \left( \frac{ct}{2} \right) \left( \frac{r\theta}{2} \right)^2 \left( 1 - \eta \right), \quad (3)$$

where $c$ = the speed of light [m s$^{-1}$], $\tau$ = radar pulse length [s], $r$ = range to the sample volume midpoint [m], and $\theta$ = beam width [radians]. Scatterer density [cm$^2$ km$^{-2}$] was then calculated by dividing total scatterer cross section in a user-selected region [cm$^2$] by the total area of that region [km$^2$]. Area was estimated assuming a downward projection of a sample volume to the surface, which is a region shaped like a partial annulus.

In many studies, a backscatter cross-section is assumed and used to estimate the total number of scatterers (e.g. individual birds) in a region of interest (e.g. Van Den Broeke 2019). Backscatter cross-section was not used in this study because (1) the identity of targets is unknown so a representative cross-section cannot be assigned, and (2) the identity of targets may change through the migration season, necessitating a temporally varying value for the backscatter cross-section. The bioscatter density calculated here is a measure which can be compared between regions at a particular time without a need to know species composition, assuming that bioscatter composition is relatively constant across the regions being analyzed.

Biomass density was compared between regions to test the hypotheses presented above. Both a basic comparison was made (e.g. percentage of radar scans with lower biomass density in the ‘wake’ region compared to the ‘ahead’ region), and more robust statistical comparison in which the difference between storm-average ‘wake’ and ‘ahead’ biomass density was calculated. Storms for which this difference exceeded the standard deviation of the ‘wake’ values for that storm were considered more statistically meaningful. The mean wake density was divided by the mean density ahead of the storm (e.g. a value < 1 indicates lower biomass density in the wake region). The use of density ratios reduces susceptibility to effects of

| Table 1. Percentage of storms showing reduced migrant density in the ‘wake’ region (compared to the ‘ahead’ region) and in the ‘away’ region (compared to the ‘approach’ region) |
|-------------------------------------------------|----------------|----------------|
| **KOAX**                                         |                |                |
| Wake versus Ahead                                 | 61.5% (n = 13) | *84.6% (n = 13)* | *73.1%* |
| Away versus Approach                              | 50.0% (n = 14) | 61.5% (n = 13)  | 55.6%  |
| **KDVN**                                         |                |                |
| Wake versus Ahead                                 | 58.8% (n = 17) | 50.0% (n = 10)  | 55.6%  |
| Away versus Approach                              | 58.8% (n = 17) | 60.0% (n = 10)  | 59.3%  |
| **KVWX**                                         |                |                |
| Wake versus Ahead                                 | 66.7% (n = 18) | *100.0% (n = 8)* | *76.9%* |
| Away versus Approach                              | *72.2% (n = 18)* | 50.0% (n = 8)  | *65.4%* |

N-values indicate the total number of storms in each population. Asterisks around a value (*) indicate significance at the 95% percentile or greater.
differing migrant density as a function of year, season, day and site. A background biomass density (BBD) value was estimated at each radar scan time within portions of the radar domain not influenced by convection.

The low-level wind is hypothesized to control the distribution of migrants, (1) by influencing average migrant density (e.g. birds are more likely to migrate with a favorable low-level wind) and (2) by influencing the distribution of migrants around convection, even if their behavior is not altered (e.g. faster speed of migrants with a more favorable low-level wind condition will increase the magnitude of the difference between the ‘wake’ and ‘ahead’ regions and between the ‘approach’ and ‘away’ regions). For this paper, the ‘low-level’ wind field was defined as the wind from the surface extending up to \( \sim 925 \) hPa (\( \sim 0.75–1 \) km altitude). A ‘favorable wind direction’ was defined assuming that migrants will move generally northward in spring and southward in fall, though this likely varies by species. A basic flow assistance measure for a tailwind was calculated for each storm following Kemp et al. (2012):

\[
\text{Flowassistance}(\text{FA}) = y \cos \theta,
\]

\( y \) is the speed of the wind, calculated here for the surface and for 925 hPa, and \( \theta \) is the difference between the wind direction and the preferred direction of movement (north in spring, south in fall). Presumably a stronger tailwind (e.g. larger flow assistance) is more favorable to migrants via energy expenditure reduction (e.g. Kemp et al. 2012), but this may be species-dependent.

**Figure 2.** Ratio of biomass density in the wake: ahead regions of all cells examined. The dashed line indicates a ratio of 1.0 (same biomass density in the wake and ahead regions). Blue circles indicate that the difference between the comparison regions was not larger than the standard deviation of the wake region values, showing a likely lack of statistical significance. Squares indicate that the difference between comparison regions was larger than the standard deviation of the wake region values (green indicates a spring storm; orange indicates a fall storm).

**Figure 3.** Ratio of biomass density in the wake: ahead regions of convective cells at KOAX versus (A) storm size (km\(^2\)); (B) storm intensity, defined here as the 90th percentile of the reflectivity factor (\( Z_{HH} \); dBZ) values associated with a convective cell, and (C) storm speed of motion (m s\(^{-1}\)). As in Figs. 2 and 3, green circles indicate spring storms and orange circles indicate fall storms, and the dashed line indicates a ratio of 1.0 (the same biomass density in the wake and ahead regions).
Results

Biomass density (BD) distribution near thunderstorms

BD on migration nights may be a function of many factors, though these were not a focus of this study. One factor is flow assistance, which was only weakly associated with BD ($r_s = 0.159$ [surface; $p = 0.168$]; $r_s = 0.089$ [925 hPa; $p = 0.442$]). Year may be important due to population fluctuations; in this study, average BD varied by 140% as a function of year. Day of the migration season could also be important. In the cases included in this study, BD generally started relatively low, peaked in early May/early October and then decreased toward the end of the migration season. Season may also be important since fall migration consists of more individuals than spring migration (e.g. Dokter et al. 2018). Fall BD was ~3 times higher at KOAX and KVWX, consistent with this expectation, while BD was similar between fall and spring at KDVN. Radar site could also influence BD since some regions have more migrants. Among the three sites used in this study, BD was ~2.5 times higher at KOAX than at KDVN and KVWX. The differences discussed here, while valid for this dataset, may also be a function of the specific set of thunderstorm events examined.

The first hypothesis tested is that a thunderstorm’s wake would be associated with a lower density of birds. In some cases, several storms were simultaneously observed to be associated with wake density reductions (e.g. Fig. 1B). Average density in storms’ wake regions was compared with the average density ahead of those cells. Average wake biomass density was reduced for 55% of all the storms analyzed in the domain of KDVN, and >70% of storms in the domains of KOAX and KVWX (Table 1). Percentage of cells showing a wake biomass reduction was higher in fall than in spring for all sites except KDVN. The occurrence of a wake biomass reduction in fall was significant at the 95% level at KOAX and KVWX (Table 1).

In Figure 2, storms with a difference between ‘wake’ and ‘ahead’ density values exceeding the standard deviation of the ‘wake’ values are indicated as squares, and other storms are indicated as circles. A majority of significantly different events (squares) lie below a value of 1, indicating a ‘wake’ biomass reduction. This reduction was most noticeable at KOAX and KVWX in the fall, with inconsistent results in spring and at KDVN (Fig. 2). At KDVN, there was a relatively even distribution around a proportion of 1 indicating little wake reduction, though all significantly different cases fell below a value of 1. Thus a wake biomass reduction may still occur at KDVN, though not as commonly as at the other sites. For six storms (~7.5%) there was a significant biomass density increase in the wake region (Fig. 2). It is possible that small birds flying through precipitation may have higher

Table 2. Spearman’s correlation between convective characteristics and migrant density wake-ahead/away-approach region density ratios for all storms analyzed

| Size | 90th Per. | Motion |
|------|-----------|--------|
| KOAX | Wake/Ahead, SPR | -0.379 | -0.330 | -0.363 |
| KOAX | Wake/Ahead, FALL | -0.390 | -0.390 | 0.071 |
| KOAX | Away/Approach, SPR | -0.125 | 0.178 | -0.565 |
| KOAX | Away/Approach, FALL | 0.225 | 0.357 | -0.291 |
| KDVN | Wake/Ahead, SPR | 0.066 | 0.005 | -0.314 |
| KDVN | Wake/Ahead, FALL | 0.321 | 0.042 | 0.067 |
| KDVN | Away/Approach, SPR | -0.267 | -0.115 | -0.105 |
| KDVN | Away/Approach, FALL | 0.006 | -0.091 | 0.430 |
| KVWX | Wake/Ahead, SPR | -0.296 | 0.102 | 0.263 |
| KVWX | Wake/Ahead, FALL | 0.429 | 0.262 | 0.191 |
| KVWX | Away/Approach, SPR | 0.267 | 0.300 | -0.160 |
| KVWX | Away/Approach, FALL | 0.191 | 0.167 | 0.738 |

Size = storm size (km²); 90th Per. = 90th-percentile reflectivity value (dBZ); Motion = storm motion (m s⁻¹). Significant p-values indicated by asterisks: * = 0.01 < $p$ < 0.05.
reflectivity leading to an artificially increased migrant density value, that land cover effects may be locally important in these cases, or that locally-enhanced convergence in the vicinity of weak convective cells increases the number of insects and therefore the population of birds that feed on insects.

It was also hypothesized that density is larger in the ‘approach’ region than in the ‘away’ region (e.g. Fig. 1C), since birds may not prefer to fly through storms while migrating. This hypothesis was supported by 50–72% of storms, with little indication that birds were consistently more likely to avoid convection in the spring or fall. Only springtime storms at KVWX supported the hypothesis at the 95% level (Table 1). Next, as described above for the ‘wake’ and ‘ahead’ regions, difference in average biomass density was calculated for the ‘approach’ and ‘away’ regions for each storm, and if that difference was larger than the standard deviation of that storm’s ‘away’ values, the storm was assigned a higher likelihood of supporting the hypothesis (Fig. 4). A majority of cases have lower average bird density in the ‘away’ region, but there are many storms for which this is not the case (Fig. 4). No repeatable pattern was found at KOAX in the spring, with a tendency for bird density to be lower in the ‘away’ region in fall. Storms with larger differences (orange squares in Fig. 4) were concentrated at ratios < 1, indicating lower bird density in the ‘away’ region. The same was generally true for KDVN and KVWX, where the hypothesis was more strongly supported than at KOAX.

Convective characteristics were examined as a possible indicator of which storms would most strongly influence the distribution of migrating birds. We hypothesize that larger storms and more intense storms are more likely to produce a BD reduction signature since they should be the most desirable for migrants to avoid. We also hypothesize that faster storm motion should be associated with a stronger wake reduction, since birds that go to the ground under a storm will return to the height of the radar beam after the storm has traveled a greater distance away. In contrast, we hypothesize that an ‘away’ region reduction in bird density should be diminished by faster storm motion, since faster-moving storms are likely more difficult for migrating birds to avoid.

Larger storms had larger migrant density differences for only some locations and seasons (Table 2). Wake signatures were weakly more apparent with larger and more intense storms at KOAX (e.g. negative correlation with storm size and 90th percentile of ZHH) regardless of season, though this relationship was more robust in fall (Fig. 3A). At KDVN and KVWX larger storms were often associated with weak wake density reductions or even density increases, contrary to the hypothesized pattern. The hypothesized greater wake density reduction with larger cells was more likely in spring than fall, though this hypothesized relationship was not well-supported. The hypothesized reduction in the ‘away’ region for larger storms was not repeatably supported (Table 2). Storms with more intense precipitation, estimated by the magnitude of the 90th percentile of ZHH values, were associated with larger wake density reductions at KOAX (Fig. 3B) in fall, but not at the other radar sites. A density reduction was not repeatedly found in stronger cells ‘away’ regions (Table 2). The hypothesized wake density reduction for faster-moving storms was weakly supported at KOAX and KDVN (e.g. Fig. 3C; Table 2). Farther east at KVWX, this association changed sign and the hypothesis was unsupported. Storm motion was associated with some significant effects in the approach versus away regions (Table 2). Fast-moving storms were associated with larger ‘away’ region deficits at KOAX, especially in spring. This pattern was weaker at KDVN and at KVWX in spring, and reversed sign at KVWX in fall ($r_s = 0.738, p = 0.046$; Table 2).

**Table 3.** Spearman’s correlation between surface (sfc)925 hPa flow assistance (FA) and migrant density (Density), and between FA and wake-ahead/approach-away region density ratios

| Site   | FA, Sfc | FA, 925 mb |
|--------|---------|------------|
| KOAX   |         |            |
| Density, SPR | -0.073  | -0.020     |
| Density, FALL | 0.561   | 0.401      |
| Wake/Ahead, SPR | 0.126   | 0.280      |
| Wake/Ahead, FALL | -0.123  | 0.165      |
| Away/Approach, SPR | 0.042   | 0.244      |
| Away/Approach, FALL | -0.610  | -0.253     |
| KDVN   |         |            |
| Density, SPR | 0.177   | 0.379      |
| Density, FALL | 0.600   | -0.049     |
| Wake/Ahead, SPR | 0.231   | 0.221      |
| Wake/Ahead, FALL | -0.115  | -0.103     |
| Away/Approach, SPR | 0.021   | -0.169     |
| Away/Approach, FALL | -0.030  | 0.310      |
| KVWX   |         |            |
| Density, SPR | 0.243   | 0.263      |
| Density, FALL | 0.571   | 0.204      |
| Wake/Ahead, SPR | 0.456   | 0.374      |
| Wake/Ahead, FALL | 0.667   | 0.323      |
| Away/Approach, SPR | -0.156  | -0.051     |
| Away/Approach, FALL | 0.405   | 0.599      |

SPR = spring storms; FALL = fall storms. Significant $p$-values indicated by asterisks: * $p < 0.05$.

**Migrant distribution and the low-level wind**

Distance from the storm of interest to the radar did not influence average migrant density in the vicinity of the
storns examined (magnitude of Pearson’s correlation ≤ 0.263 for each radar site and 0.021 for the whole dataset; not shown). This indicates that the storm-radar distance was not a dominant factor influencing the observed distribution of migrants for the storms included in this study.

Migration density was more strongly associated with flow assistance in fall than in spring at all sites (Table 3). Fall migration density was primarily a function of surface flow assistance, with relatively weak association between migration density and 925-hPa flow assistance. Larger values of surface flow assistance (stronger tailwind) correspond to larger migration density (Table 3). Spearman’s correlation between these variables was generally much lower in spring for this sample of events. The correlation between surface flow assistance and fall migration density was statistically significant at KOAX \( r_s = 0.601, \ p = 0.039 \).

Since flow assistance appears to primarily influence fall migrant density, convection is hypothesized to more strongly influence migrant decisions when the low-level wind is favorable for migration especially in fall, since convection often represents a marked disruption of the low-level wind field. The distribution of migrants in the wake and ahead regions of convection was not always consistent with this hypothesis, with strongest associations in fall at KVWX (the east side of the study domain), where large wake migrant deficits were generally observed with smaller flow assistance values (Table 3). Little association between flow assistance and migrant distribution in the ‘wake’/’ahead’ regions was noted at KOAX or KDVN.

Patterns in the ‘away’/’approach’ regions of convection were stronger in fall than in spring. Little trend was observed in spring for all sites (Table 3). In fall, large flow assistance values at the surface were associated with larger ‘away’ region biomass density reductions at KOAX; this result was statistically significant at the 95th percentile. Little pattern was evident at KDVN. Farther east at KVWX, the opposite pattern was observed compared to KOAX, and it was most notable at 925 hPa (Table 3).

**Discussion**

Birds are expected to migrate when some set of factors is favorable, likely including weather conditions, and to make decisions about where to travel and when to land. Thunderstorms may be one factor necessitating migrating birds to reroute or land. In this study, the biomass density distribution was examined around a sample of isolated storms in the domains of three radar sites, with a goal of determining how often and under what conditions migrants modify their distribution because of convection. The migrant distribution proximate to convection may provide insight on decision-making by migrants to avoid potential convective hazards.

Consistently reduced density of migrants is indicated in the wake of storms in eastern Nebraska (KOAX) and southern Indiana (KVWX), with less consistent evidence for this behavior in eastern Iowa (KDVN). Migrant density was reduced in the wake of larger storms and storms with more intense precipitation only in eastern Nebraska. This may reflect the larger climatological frequency of significant severe weather (large hail, strong wind) on the Great Plains compared to farther east (e.g. Cintineo et al. 2012; Smith et al. 2013), which may make migrants more likely to avoid intense storms in that region. Faster-moving storms were associated with larger wake density reductions in eastern Nebraska and eastern Iowa, possibly because these storms move farther in the same amount of time, assuming it takes the same amount of time for a grounded migrant to regain flight altitude. There is strong evidence that many storms either ground migrants or that migrants avoid the storm wake region, and therefore a wake reduction in migrant density occurs after those storms move away. Several large and/or intense storms were seen which did not display a wake signature – factors explaining whether a storm will influence the migrant distribution are not yet fully understood.

The ‘approach’/’away’ regions showed generally weak signals of migrant distribution changes in response to convective characteristics except for storm motion. Fast-moving spring storms were associated with larger ‘away’ region biomass reduction at KOAX, and slower-moving fall storms were associated with larger biomass reduction at KVWX. Overall, the weak changes to the distribution of migrants in the ‘approach’/’away’ regions as a function of storm characteristics could indicate that migrants may not alter their path as they approach a storm. This may be consistent with prior research which has noted substantial mortality of birds in thunderstorms (e.g. Wiedenfeld and Wiedenfeld 1995; Diehl et al. 2014). It is unknown if migrants approaching a storm typically slow down and wait for it to move on, if they typically detour, or if they take no action. A detailed study of the \( V_r \) field near convection might provide insight about these smaller-scale migrant decisions.

A comparison of migration characteristics as a function of flow assistance showed that migrants are more strongly and consistently influenced by wind conditions in fall than in spring. This supports the idea that in spring, birds are obligated to cover a set distance in a certain amount of time so they can arrive on their breeding grounds (e.g. Newton 2012). In fall, however, birds appear more likely to wait for favorable migration conditions before moving.

Higher migration density was expected with large flow assistance (e.g. stronger wind from the south [north] in
the spring [fall]), minimizing energy expenditure. This expected association was found for all three radar sites, but generally only for surface flow assistance in fall. Flow assistance at 925 hPa was only weakly associated with migration density. Given the surface elevation and assuming standard radar beam propagation, the 925-hPa pressure level is ~39 km from the radar site at KOAX, ~49 km from KDVN, and ~50 km from KVWX. A majority of storms analyzed were above the typical 925-hPa altitude on average (89% at KOAX, 63% at KDVN, 54% at KVWX), though their wind fields could extend to the surface. These results indicate that birds’ decision to migrate is based primarily on the surface wind conditions.

Distribution of migrants around convection was most strongly a function of the wind in fall, again suggesting the lesser importance of springtime environmental conditions. In general, larger wake density reductions were observed with larger flow assistance values in Nebraska, but this pattern was weak or reversed in eastern Iowa and southern Indiana. It is unknown whether these findings indicate a gradient of behavior possibly related to species composition, or if they are a result of the relatively small sample sizes. Lower migrant density in storm ‘away’ regions was most commonly observed in eastern Nebraska, possibly indicating that birds there are more likely to land to avoid convection if the background wind field is not as favorable for migration. This pattern was only seen in fall, supporting the lesser importance of springtime environmental conditions.

Several study limitations should be more thoroughly addressed in future studies with larger samples. First, the small sample sizes for many of the fall periods analyzed decrease the results’ statistical robustness. Given the relatively narrow definition of storms analyzed, it will be challenging to develop larger samples until additional radar data are available in the future. Storm-radar distance may influence the findings, but in this study this factor did not appear to contribute appreciably to variability in the results. Distance could especially be a factor when there are strong gradients of migrant density upward from the surface. This causes migrant density to change quickly going outward from the radar site, since the radar beam gets higher with distance. There would also be value in examining other meteorological contributors to migrant density, which could increase our understanding of the synoptic weather regimes under which birds are most likely to migrate, which are likely to differ between spring and fall.

The results presented here demonstrate that weather conditions influence the density of migrants, particularly in fall when migrants are not obligated to cover distance quickly. It has also been demonstrated that migrants may be influenced by thunderstorms, and may either decide to avoid convection or may be forced to land while convection goes overhead. Future studies examining more details of migrant behavior in the vicinity of thunderstorms would be beneficial to understand how migrants make decisions about their surroundings and potential threats encountered during migration.

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**Data Availability Statement**

Radar data are available for free at the National Centers for Environmental Information (https://www.ncdc.noaa.gov/has/HAS.FileAppRouter?datasetname=6500&subquery=STATION&appliance=&outdest=FILE) or the Amazon Web Services Level 2 NEXRAD archive (https://s3.amazonaws.com/noaa-nexrad-level2/index.html). Environmental data, including the surface and upper-air observations used here, are accessible from the National Climatic Data Center (https://www.ncdc.noaa.gov/cdo-web/datatools/findstation) and from the University of Wyoming sounding archive (http://weather.uwyo.edu/upperair/sounding.html).

**References**

Bellrose, F. C. 1957. A spectacular waterfowl migration through central North America. Biological Notes No. 36, Natural History Survey Division, Urbana, IL, 24 pp.

Bellrose, F. C. 1968. Waterfowl migration corridors east of the Rocky Mountains in the United States. Biological Notes No. 61, Illinois Natural History Survey, Urbana, IL, 24 pp.

Berthold, P. 2001. Bird migration: a general survey, 2nd edn. Oxford University Press. 253 pp.

Bildstein, K. L., J. P. Smith, E. Ruelas Inzunza, and R. R. Veit, eds. 2008. State of North America’s Birds of Prey. Series in Ornithology 3. Nuttall Ornithological Club, Cambridge, MA, and American Ornithologists’ Union, Washington, D.C., 466 pp.
Bonter, D. N., S. A. Jr. Gauthreaux, and T. M. Donovan. 2009. Characteristics of important stopover locations for migratory birds: remote sensing with radar in the Great Lakes basin. *Conserv. Biol.* 23, 440–448.

Both, C. 2010. Flexibility of timing of avian migration to climate change masked by environmental constraints en route. *Curr. Biol.* 20, 243–248.

Buler, J. J., and D. K. Dawson. 2014. Radar analysis of fall bird migration stopover sites in the northeastern U.S. *Condor* 116, 357–370.

Chapman, J. W., V. A. Drake, and D. R. Reynolds. 2011. Recent insights from radar studies of insects. *Annu. Rev. Entomol.* 56, 337–356.

Chilson, P. B., W. F. Frick, P. M. Stepanian, J. R. Shipley, T. H. Kunz, and J. F. Kelly. 2016. Estimating animal densities in the atmosphere using weather radar: To Z or not to Z? *Ecosphere* 3, 1–19.

Cintineo, J. L., T. M. Smith, and V. Lakshmanan. 2012. An objective high-resolution hail climatology of the contiguous United States. *Weather Forecast* 27, 1235–1248.

Diehl, R. H., J. M. Bates, D. E. Willard, and T. P. Gnoske. 2014. Bird mortality during nocturnal migration over Lake Michigan: a case study. *Wilson J. Ornithol.* 126, 19–29.

Dokter, A. M., A. Farnsworth, D. Fink, V. Ruiz-Gutierrez, W. M. Hochachka, F. A. La Sorte, et al. 2018. Seasonal abundance and survival of North America’s migratory avifauna determined by weather radar. *Nature Ecology and Evolution* 2, 1603–1609.

Eisaguirre, J. M., T. L. Booms, C. P. Barger, C. L. McIntyre, S. B. Lewis, and G. A. Breed. 2018. Local meteorological conditions reroute a migration. *Proceedings of the Royal Society B: Biological Sciences* 285: 20181779.

Fourment, M., A. E. Darling, and E. C. Holmes. 2017. The impact of migratory flyways on the spread of avian influenza virus in North America. *BMC Evol. Biol.* 17, 118.

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

Gauthreaux, S. A., C. G. Belser, and D. van Blaricom. 2003. Using a network of WSR-88D weather surveillance radars to define patterns of bird migration at large spatial scales. *in P. Berthold, E. Gwinner and E. Sonnenschein, eds. Avian Migration*, Springer, Berlin, Heidelberg.

Gauthreaux, S. A., J. W. Livingston, and C. G. Belser. 2008. Detection and discrimination of fauna in the atmosphere using Doppler weather surveillance radar. *Integr. Comp. Biol.* 48, 12–23.

Gauthreaux, S. A., D. S. Mizrahi, and C. G. Belser. 1998. Bird migration and bias of WSR-88D wind estimates. *Weather Forecast.* 13, 465–481.

Kemp, M. U., J. Shamoun-Baranes, E. E. van Loon, J. D. McLaren, A. M. Dokter, and W. Bouten. 2012. Quantifying flow-assistance and implications for movement research. *J. Theor. Biol.* 308, 56–67.

Kerlinger, P., and F. R. Moore. 1989. Atmospheric structure and avian migration. Pp. 109–142. *Current Ornithology*. Springer, Boston, MA.

Kölzsch, A., S. Bauer, R. de Boer, L. Griffin, D. Cabot, K.-M. Exo, et al. 2014. Forecasting spring from afar? Timing of migration and predictability of phenology along different migration routes of an avian herbivore. *J. Anim. Ecol.* 84, 272–283.

Lisovski, S., H. Schmaljohann, E. S. Bridge, S. Bauer, A. Farnsworth, S. A. Gauthreaux, et al. 2018. Inherent limits of light-level geolocation may lead to over-interpretation. *Curr. Biol.* 28, R99–R100.

Mills, A. M. 2005. Changes in the timing of spring and autumn migration in North American migrant passerines during a period of global warming. *The Ibis* 147, 259–269.

Nadal, J., C. Ponz, and A. Margalida. 2018. Synchronizing biological cycles as key to survival under a scenario of global change: the Common Quail (*Coturnix coturnix*) strategy. *Sci. Total Environ.* 613–614, 1295–1301.

Newton, I. 2012. Obligate and facultative migration in birds: Ecological aspects. *J. Ornithol.* 153, 171–180.

Niemuth, N. D., M. E. Estey, R. E. Reynolds, C. R. Loech, and W. A. Meeks. 2006. Use of wetlands by spring-migrant shorebirds in agricultural landscapes of North Dakota’s drift prairie. *Wetlands* 26, 30–39.

O’Neal, B. J., J. D. Stafford, and R. P. Larkin. 2012. Stopover duration of fall-migrating dabbling ducks. *J. Wildl. Manage.* 76, 285–293.

O’Neal, B. J., J. D. Stafford, and R. P. Larkin. 2014. Migrating ducks in inland North America ignore major rivers as leading lines. *The Ibis* 157, 154–161.

Parish, T. R., A. R. Rodi, and R. D. Clark. 1988. A case study of the summertime Great Plains low level jet. *Mon. Weather Rev.* 116, 94–105.

Park, H., A. V. Ryzhkov, D. S. Zrnić, and K.-E. Kim. 2009. The hydrometeor classification algorithm for the polarimetric WSR-88D: description and application to an MCS. *Weather Forecast* 24, 730–748.

Rosenberg, K. V., A. M. Dokter, P. J. Blancher, J. R. Sauer, A. C. Smith, P. A. Smith, et al. 2019. Decline of the North American avifauna. *Science* 366, 120–124.

Serie, J. R., D. L. Trauger, and D. E. Sharp. 1983. Migration and winter distributions of Canvasbacks staging on the Upper Mississippi River. *J. Wildl. Manage.* 47, 741–753.

Shamoun-Baranes, J., F. Liechti, and W. M. G. Vansteelandt. 2017. Atmospheric conditions create freeways, detours and tailbacks for migrating birds. *J. Comp. Physiol. A.* 203, 509–529.

Smith, B. T., T. E. Castellanos, A. C. Winters, C. M. Mead, A. R. Dean, and R. L. Thompson. 2013. Measured severe convective wind climatology and associated convective modes of thunderstorms in the contiguous United States, 2003–09. *Weather Forecast.* 28, 229–236.
Smith, R. V., J. D. Stafford, A. P. Yetter, M. M. Horath, C. S. Hine, and J. P. Hoover. 2012. Foraging ecology of fall-migrating shorebirds in the Illinois River valley. *PLoS One* **7**, e45121.

Streby, H. M., G. R. Kramer, S. M. Peterson, J. A. Lehman, D. A. Buehler, and D. E. Andersen. 2015. Tornadic storm avoidance behavior in breeding songbirds. *Curr. Biol.* **25**, 98–102.

Streby, H. M., G. R. Kramer, S. M. Peterson, J. A. Lehman, D. A. Buehler, and D. E. Andersen. 2018. Response to Lisovski, et al. *Curr. Biol.* **28**, R101–R102.

Van Buskirk, J., R. S. Mulvihill, and R. C. Leberman. 2009. Variable shifts in spring and autumn migration phenology in North American songbirds associated with climate change. *Glob. Change Biol.* **15**, 760–771.

Van Den Broeke, M. S. 2013. Polarimetric radar observations of biological scatterers in Hurricanes Irene (2011) and Sandy (2012). *J. Atmos. Ocean Tech.* **30**, 2754–2767.

Van Den Broeke, M. S. 2019. Radar quantification, temporal analysis, and influence of atmospheric conditions on a roost of American Robins (*Turdus migratorius*) in Oklahoma. *Remote Sens Ecol Conserv.* **5**, 193–204.

Van Doren, B. M., and K. G. Horton. 2018. A continental system for forecasting bird migration. *Science* **361**, 1115–1118.

Vansteelandt, W. M. G., J. Shamoun-Baranes, J. McLaren, J. van Dierman, and W. Bouten. 2017. Soaring across continents: decision-making of a soaring migrant under changing atmospheric conditions along an entire flyway. *J. Avian Biol.* **48**, 887–896.

Vaughn, C. R. 1985. Birds and insects as radar targets: A review. *Proc. IEEE* **73**, 205–227.

Wainwright, C. E., P. M. Stepanian, and K. G. Horton. 2016. The role of the US Great Plains low-level jet in nocturnal migrant behavior. *Int. J. Biometeorol.* **60**, 1531–1542.

Weber, T. P., and A. I. Houston. 1997. Flight costs, flight range and the stopover ecology of migrating birds. *J. Anim. Ecol.* **66**, 297–306.

Wiedenfeld, D. A., and M. G. Wiedenfeld. 1995. Large kill of neotropical migrants by tornado and storm in Louisiana, April 1993. *J. Field Ornithol.* **66**, 70–80.

**Supporting Information**

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

**Appendix S1.** The date and analysis period (UTC) for all storms included in this study