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RESEARCH ARTICLE

Migrating birds reorient toward land at dawn over the Great Lakes, USA

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ABSTRACT

Most landbirds migrate at night and typically make landfall in suitable stopover habitat before dawn. However, when birds find themselves over large water bodies at dawn, they must continue flying into the day and either finish crossing the water body and land on the far shore or backtrack to the near (i.e. first encountered) shore to land. Their collective decisions will influence how migrants are distributed among shoreline stopover habitats on either side of the water crossing. We studied birds during 4 spring migration seasons from 2010 to 2013 in the Great Lakes region, USA. We used 3 weather surveillance radars to observe migrating landbirds' behavior at dawn and subsequent terrestrial distributions during stopover. Mean flight heights over land and water were higher and mean flight directions were more oriented toward the closest shore at dawn when compared to peak migration earlier in the night. The wider the lake crossing, the higher that birds along the lakeshore flew at dawn. Seasonal mean stopover densities of migrants on land within 3 km of shorelines were 48% higher on the near shores of lakes (based on the seasonal mean direction of migration) than on the far shores. There was a moderate positive correlation ($r = 0.584$, $P < 0.001$, $n = 358$) between the seasonal mean density of birds aloft over water at dawn and the stopover density of birds in adjacent shorelines. Thus, birds over the water at dawn may tend to return to the near shore of the Great Lakes for stopover rather than continuing across the water. As a result, shoreline habitats on the near shores of lakes harbor greater densities of migrants and are thus critical stopover sites for migrating landbirds in the Great Lakes region.

Keywords: flight behavior, Great Lakes, migration, radar, shoreline, stopover

Aves migratorias se reorientan hacia la tierra al amanecer sobre los Grandes Lagos

RESUMEN

La mayoría de las aves terrestres migran durante la noche y típicamente paran en hábitats adecuados antes del amanecer. Sin embargo, cuando las aves se hallan sobre grandes cuerpos de agua al amanecer, deben seguir volando entrado el día y terminar de cruzar el cuerpo de agua y aterrizar en la orilla del lado opuesto o dar marcha atrás hasta la orilla que encontraron en primera instancia para aterrizar. Sus decisiones colectivas van a influenciar el modo en que las aves migratorias están distribuidas entre los ambientes de parada en las orillas a cada lado de las aguas atravesadas. Estudiamos aves durante cuatro estaciones migratorias de primavera desde 2010 a 2013 en la región de los Grandes Lagos. Usamos tres radares de vigilancia climática para observar el comportamiento de las aves terrestres migratorias al amanecer y las subsecuentes distribuciones terrestres cerca de la orilla durante la parada. Las alturas promedio del vuelo sobre la tierra y el agua fueron más elevadas y las direcciones promedio de vuelo estuvieron más orientadas hacia la primera orilla encontrada al momento del amanecer en comparación con el pico de migración que ocurre más temprano en la noche. Cuanto más ancho fue el lago que cruzaron, más alto volaron las aves a lo largo de la orilla del lago al amanecer. Las densidades estacionales promedio en los sitios de parada a menos de 3 km de la orilla fueron 48% más altas en la orilla primeramente encontrada de los lagos usando la dirección estacional promedio de los migrantes en comparación con el lado opuesto de los lagos. Encontramos una correlación positiva moderada ($r = 0.584$, $n = 358$, $p < 0.001$) entre la densidad estacional promedio de las aves sobre el agua al amanecer y la densidad de aves en los sitios de parada en las orillas adyacentes. Por ende, las aves sobre el agua al amanecer tienden a regresar a las orillas encontradas en primera instancia de los Grandes Lagos para parar, más que seguir a través del agua. Como resultado, los hábitats de las orillas encontradas en primera instancia de los lagos albergan densidades mayores de migrantes y son por ende sitios críticos de parada para las aves migratorias terrestres en la región de los Grandes Lagos.

Palabras clave: comportamiento de vuelo, Grandes Lagos, migración, orilla, radar, sitio de parada

INTRODUCTION

The Great Lakes region of the United States is an important stopover area for migrating landbirds in both spring and fall (Bonter et al. 2009). High concentrations of birds are generally present in stopover habitat along the shores of the lakes and have been linked to the presence of abundant food sources in these habitats (Smith et al. 2007, Ewert et al. 2011). The majority of research in this area has focused on characteristics of stopover habitat use (e.g., Ewert and Hamas 1996, Smith et al. 2004, 2007, Rodewald and Matthews 2005, Bonter et al. 2009, Ewert et al. 2011). The link between flight behaviors of migrating landbirds aloft over the lakes and distributions within stopover habitat is less well understood.

The U.S. network of weather surveillance radars, comprising model Weather Surveillance Radar–1988 Doppler (WSR-88D) or Next Generation Radar (NEXRAD), is a powerful tool to study birds in the air (Gauthreaux and Belser 1998). Diehl et al. (2003) used NEXRAD to observe a flight behavior they dubbed “dawn ascent” in the Great Lakes region. Dawn ascent is characterized by migrating birds over the water, increasing their flight height and often reorienting themselves toward shorelines as dawn approaches. Diehl et al. (2003) reported the median range over which reorientation occurred as ~28 km from the shore, although increased flight heights were observed over longer distances. Dawn ascent and reorientation has also been observed along the North Sea (Myres 1964). Dawn ascent could be a response to migrating birds’ reluctance to continue a water crossing, regardless of the crossing distance, into daylight hours; nocturnal migrants typically end their flights at dawn (Diehl et al. 2003). Birds may gain altitude in an effort to locate the nearest shoreline or evaluate how far they must travel to complete a water crossing. If birds are returning to shore at dawn, this could contribute to the higher concentrations of birds along shorelines first encountered by birds when approaching the lake from the dominant seasonal migratory direction (hereafter “near shores”). Non-reoriented crossing will tend to direct birds toward shorelines encountered after crossing the lake in the dominant seasonal migratory direction (hereafter “far shores”). However, no studies have yet linked stopover distributions to the dawn-ascent flight behavior of migrants along the Great Lakes. Additionally, there have not been detailed studies of broad-scale variability in dawn flight behavior, nor of stopover use along shorelines that may depend on whether birds need to turn back or continue forward to reach the nearest shoreline.

In the present study, we used NEXRAD data from the Great Lakes region of the United States to compare the flight behaviors (height and direction) of migrating landbirds aloft over land and over water at peak migration and at dawn. We

also measured the density of birds aloft over stopover habitat within 3 km of the shores of the Great Lakes at dawn over water and during exodus over land and tested whether differences between densities on the near and far shores of the lakes are linked to dawn flight behavior.

We hypothesized that migrating birds would show differences in flight behavior at dawn compared to peak migration earlier in the night. We expected birds at dawn to show (1) increased flight heights and (2) flight directions more oriented toward the near shores of the Great Lakes, compared to the patterns at peak migration (Diehl et al. 2003). We further hypothesized that migrating birds over water at dawn might show additional differences in flight characteristics—increased height and reoriented flight direction—with respect to birds over land at dawn. The hypothesized changes in flight behavior might indicate that birds at dawn are looking for stopover habitat on the near shores of the lakes, which should result in measureable differences in stopover patterns of emigrants at flight exodus on following nights. Accordingly, we expected to see increased densities of birds at exodus on the near shores of the Great Lakes, as well as positive correlations between densities of birds over water at dawn and densities of birds over land at exodus the following night.

A more complete understanding of dawn ascent in the Great Lakes region illuminates the relationship between the behavior of birds aloft and stopover habitat selection, especially in habitat on the near shores. This information can inform decisions about the preservation of stopover habitat and the conservation of migratory birds in the Great Lakes.

METHODS

We used data collected from 3 NEXRAD stations across the Great Lakes region of the United States: Cleveland, Ohio (KCLE: 41.413°N, 81.859°W); Grand Rapids, Michigan (KGRR: 42.893°N, 85.544°W); and Green Bay, Wisconsin (KGRB: 44.498°N, 88.111°W) (Figure 1). These radars were selected because they observed significant amounts of Great Lakes shoreline (i.e. Lake Michigan and Lake Erie). We analyzed data collected by each radar during the spring migration season, April 1 to June 15, from 2010 to 2013. For each sampling day, we analyzed radar data from each station collected at 3 time points: (1) the onset of nocturnal migration exodus, hereafter “exodus”; (2) ~3 hr after sunset during the typical peak of migratory flight (Gauthreaux and Belser 1998, Diehl et al. 2003), hereafter “peak migration”; and (3) at dawn (sun elevation at the horizon). For sampling at peak migration and at dawn, we used the single radar volume scan closest in time to the desired time point. For sampling at migration exodus, we interpolated radar data in between volume scans using simple distance-weighted averaging for

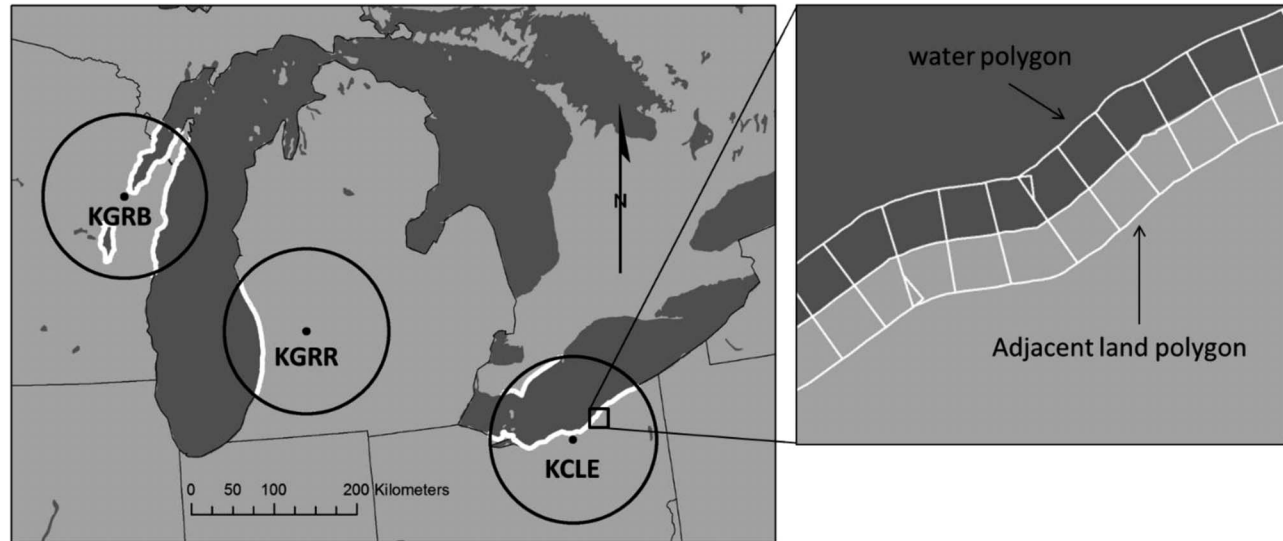


FIGURE 1. Locations and names of the 3 NEXRAD stations in the Great Lakes region, USA, that were used in the study. Radar coverages of data are within the black rings. The shoreline for which data were collected is highlighted in white. The inlay shows how the shoreline was broken into polygons of 3 km parallel by 3 km perpendicular to shorelines to cover the area of water (dark gray) and an adjacent area of land (light gray) to compare reflectivity at dawn over water and at exodus over land.

every radar sampling volume to the time when the sun's elevation angle reached 7° below the horizon (i.e. just after the end of evening civil twilight; *sensu* Buler and Dawson 2014). When comparing data gathered at these time points, "peak migration" refers to the evening prior to a dawn sample and "exodus" refers to the evening following a dawn sample.

We constructed a shapefile in a geographic information system (GIS) to delineate shoreline segments of large lakes near each radar station. The shapefile consisted of polygons that were each 3 km parallel and 3 km perpendicular to the shoreline, covering a 9 km^2 area of either land or water on either side of the shoreline boundary (see inset of Figure 1). This shapefile was intersected with polar coordinate polygon basegrids of radar sampling volumes extending in a 100 km radius around each radar station to identify the portions of specific sampling volumes within each shoreline segment. The basegrid for each radar station is a GIS shapefile that delineates the two-dimensional boundaries of individual radars' sampling volumes within the coverage area of the radar, allowing the reflectivity data collected by the radar to be transformed into a geographic state space. Sampling volumes of radar basegrids have an azimuthal resolution of 0.5° and range resolution of 250 m, corresponding with the resolution of NEXRAD. We also characterized each shoreline segment by side of the lake, such that "near shores" are the shorelines typically encountered by birds before crossing a lake while flying along their mean peak migration track (Table 1) during the spring migration season, and "far shores" are the shorelines typically

encountered by birds after crossing a lake. Near shores were those on the eastern and southern sides of the Great Lakes; far shores were those on the western and northern sides. The domain of the Grand Rapids radar covered only near shores, while the Green Bay and Cleveland radars had a mix of near and far shores.

Radar Data Processing

Radar volume scans measuring birds aloft went through a two-stage screening process to determine suitability. First, we visually screened radar imagery compiled at the Surveillance of the Atmosphere Using Weather Radar (SOAR) website (<http://soar.ou.edu/legacy.html>) to achieve a coarse filter for contamination. SOAR provides a fast and easy-to-access look at the radar data but is limited by a coarse resolution and overlapping data from adjacent radar stations. The 2 main sources of contamination were precipitation and anomalous propagation, in which certain atmospheric conditions cause excessive refraction of the radar beam. We excluded from further analyses scans with precipitation within 100 km of the radar, or with obvious anomalous propagation of the beam. We downloaded radar sweeps that passed this first round of screening from the National Climatic Data Center (<http://has.ncdc.noaa.gov/pls/plhas/has.dsselect>), a service of the National Oceanic and Atmospheric Administration. Radar sweeps were visually screened at their native resolution for precipitation and anomalous propagation a second time with the program Integrated Data Viewer (Murray et al. 2003) to verify their suitability for analysis.

TABLE 1. Mean values (\pm SE) for flight characteristics of migrating birds in the Great Lakes region, USA, at dawn and at peak migration earlier that night as detected by 3 radars, 2010–2013.

| Flight characteristic | | | Radar | | | | |
|--------------------------|--------------------------------|----------------|----------------|----------------|-----------------|-------------------|---|
| Metric | Time | Location | KCLE | KGRB | KGRR | All radars pooled | |
| Height above surface (m) | Peak migration | Land | 574 \pm 57.9 | 489 \pm 38.6 | 615 \pm 70.2 | 542 \pm 30 | |
| | | Water | 681 \pm 79.2 | 441 \pm 45.5 | 522 \pm 36.1 | 525 \pm 34.7 | |
| | Dawn | Land | 565 \pm 15.9 | 734 \pm 14.7 | 980 \pm 7.2 | 704 \pm 17.2 | |
| | | Water | 664 \pm 15.5 | 812 \pm 14.4 | 1022 \pm 4.6 | 785 \pm 15.4 | |
| | Track direction ($^{\circ}$) | Peak migration | Land | 27.6 \pm 0.2 | 349.7 \pm 0.1 | 345.2 \pm 0.1 | – |
| | | | Water | 24.7 \pm 0.3 | 329.9 \pm 0.2 | 332.9 \pm 0.2 | – |
| Dawn | | Land | 83.0 \pm 1.3 | 16.1 \pm 1.0 | 54.1 \pm 0.5 | – | |
| | | Water | 89.1 \pm 1.3 | 2.4 \pm 0.9 | 65.3 \pm 0.4 | – | |

We used the Weather Decision Support System–Integrated Information (WDSS-II), a suite of algorithms for weather radar data analysis (available at <http://www.wdsii.org>), to convert raw radar files into netCDF format containing reflectivity and radial velocity measures. We used data from the 0.5° beam tilt-angle sweep because this was the angle at which most birds were observed by the radar and because data at higher tilt angles were too sparse to be useful.

We used a Matlab program written by Dan Sheldon of the University of Massachusetts Amherst and NASA's Radar Software Library to de-alias the velocity data (Farnsworth et al. 2014). We then used custom R code to produce a velocity azimuth display (VAD) profile from each range annulus of each 0.5° sweep (*sensu* Browning and Wexler 1968). The VAD profile fits a sine function through the radial velocity data to give an average ground speed and track direction of flight for animals at the mean height of the radar beam above ground within each range annulus. The accuracy of the VAD assumes that animals are moving in a consistent manner, however variable their directions and speeds, throughout the altitudinal strata being analyzed. We excluded from analyses heights at which $R^2 < 0.25$ for the modeled sine functions. We retrieved VAD profiles separately for data over land and over water for each of our time periods: dawn, exodus, and peak migration.

We computed the mean ground speed and direction of birds across the VAD for each sweep by weighting data from each height using a vertical profile of reflectivity (VPR) following Buler and Dawson (2014). The VPR describes the ratio of the vertical variability of reflectivity at a given height in relation to the mean reflectivity from the ground to 1,750 m above the ground and was also used to determine the mean flight height of birds. These metrics were computed such that we had a measure of mean flight height and direction of birds for each radar sweep. Mean flight height and direction for each sweep were computed across all data within the range of radar, separating only into data collected over land and over water. We applied 3 grouping variables to

the data: radar (KCLE, KGRB, KGRR), location (land vs. water), and time (dawn vs. peak migration). To distinguish the dominant biota aloft, we performed VAD analysis of radial velocity from the 3.5° tilt-angle radar sweep sampled at peak migration and subtracted wind vector from winds aloft collected via nearby radiosonde (archived by the University of Wyoming) or from surface winds collected from nearby weather stations when radiosonde data were not available to calculate mean target airspeeds. All nights with mean target airspeeds $< 5 \text{ m s}^{-1}$ were considered insect dominated and were eliminated from analyses (Larkin 1991).

We estimated the vertically integrated reflectivity (VIR) within each sample volume in order to directly compare reflectivity measures at different ranges from radars and among radar scans, following previously established methods (Buler and Diehl 2009, Buler and Dawson 2014). This approach is necessary because the radar beam systematically samples increasing heights as it propagates away from the radar and because the vertical profile of bird reflectivity varies among radar scans. Each raw reflectivity measure is divided by the mean VPR ratio within the sampled volume airspace to produce an estimate of the mean reflectivity of birds in the airspace from 0 to 1,750 m above the ground. We converted the original reflectivity factor in units of Z ($\text{mm}^6 \text{ m}^{-3}$) into more biologically meaningful units ($\text{cm}^2 \text{ km}^{-3}$; Chilson et al. 2012). We then multiplied reflectivity by the height of 1,750 m to “flatten” the volumetric measure of reflectivity into a two-dimensional measure ($\text{cm}^2 \text{ ha}^{-1}$) representing the total amount of reflected cross-sectional area of birds per hectare above the ground. Unlike the analysis of flight height and direction, for which a mean value was computed for migrants over land and over water at each time point, mean VIR was computed individually within each shoreline polygon.

Statistical Analysis

To investigate the effects of our 3 grouping variables on flight height, we used an analysis of variance (ANOVA)

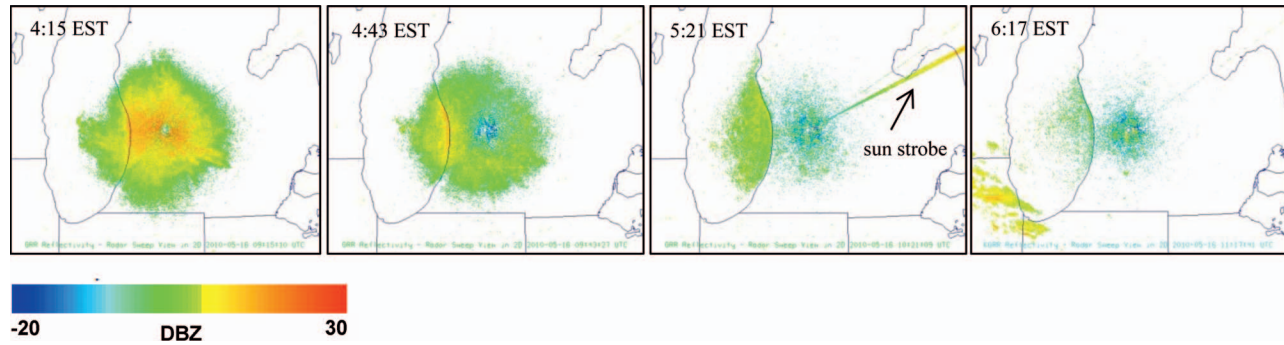


FIGURE 2. Time series of radar reflectivity from KGRR, Great Lakes region, USA, on May 16, 2010, around sunrise, showing changes in migrating birds' activity. At 4:15 EST, birds are migrating to the northwest. The sun strobe at 5:21 EST indicates sunrise. Bird activity decreases over land as birds end their migratory flight before dawn, whereas birds over water remain aloft after dawn.

with 3 factors: radar (KCLE, KGRB, KGRR), time (dawn, peak migration), and location (over land, over water). We used a Tukey-Kramer post hoc test to investigate differences between individual groups. To investigate the effects of our 3 grouping variables on flight directions, we used a Harrison-Kanji test for the analysis of variance of circular data (Harrison and Kanji 1988). Because the Harrison-Kanji build in Matlab handles only 2 grouping factors, we implemented the test separately for each radar, using time and location as factors.

Area-weighted mean dawn VIR was computed for each shoreline segment over water and for each segment over land at the following exodus for every sampling day. Only days that had data for both dawn and evening exodus were included. We also computed the geometric mean of daily reflectivity for each segment across all seasons. We tested for differences in the magnitude of VIR, using shoreline (near, far) and time (dawn, exodus) as grouping factors. Because there was significant interaction between these factors, we also used independent one-way ANOVA to test the effect of shoreline separately at dawn and at exodus.

We calculated the mean VIR across all seasons for near- and far-shoreline segments with all 3 radars pooled. We used the Pearson correlations between adjacent land and water segments to assess relationships between reflectivity at dawn over water and reflectivity during the following evening exodus over land. We computed correlations between segment pairs for all shorelines together, and also for near and far shorelines separately.

RESULTS

After screening for contamination by precipitation, anomalous propagation, and insects, 15% of total potential days had suitable sweeps at dawn for analysis (KCLE: 52 days, KGRB: 39 days, KGRR: 23 days). KCLE provided data within 104 segments along 312 km of shoreline, KGRB provided data within 174 segments along 517 km of

shoreline, and KGRR provided data within 47 segments along 141 km of shoreline. The total sample size pooled across radars was 325 segments along 970 km of shoreline.

Visual inspection of time series of radar scans showed an increase in the extent and magnitude of reflectivities over the water just before dawn (Figure 2), which is consistent with migrating birds increasing their flight heights. This increase in reflectivity over water was typically not matched by a similar increase in reflectivities over land.

Differences in Flight Height and Direction

Birds showed increased flight heights at dawn compared to peak migration at the KGRB and KGRR radars, but not at KCLE (Table 1). The effects of radar and time were both significant, and an interaction between these factors was present. The effect of time (difference between dawn flight heights and peak migration flight heights) is therefore dependent on radar, with increases in dawn flight height seen at KGRB and KGRR but not at KCLE (Figure 3). The estimated mean difference in flight height between birds at dawn and birds at peak migration was 265 m at KGRB and 390 m at KGRR. The mean heights of birds aloft over water at dawn were generally great enough for birds to potentially see the opposite shoreline of lakes they were over (Table 2). In addition, these mean heights increased with increasing width of lake among the radars.

Additionally, the mean flight height over water at dawn was higher than the mean flight height over land at dawn, both at each radar individually and pooled across all samples. This effect was not present at peak migration (Table 1). Overall, the effect of location (land vs. water) was not statistically significant across all grouping variables, but there was a significant interaction term between location and time, indicating that the effect of location on flight height was different at dawn than at peak migration (Table 3).

Flight directions during peak migration were approximately northerly, ranging from 345° at KGRR to 27° at

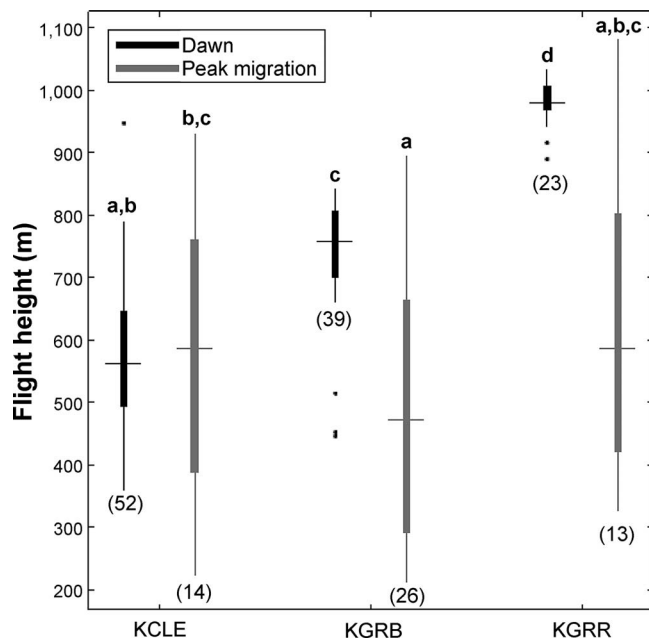


FIGURE 3. Boxplots of the flight heights for birds at dawn and during peak migration in the Great Lakes region, USA, 2010–2013. Boxes are centered at median and extend from the 25th to the 75th percentiles of the data. Whiskers extend to the extreme data points not considered outliers. Outliers are plotted separately. Sample sizes are given below the boxes. Letters indicate groups based on a Tukey-Kramer post hoc test for significant difference between groups. Boxes with the same letter are not significantly different.

KCLE. The flight directions at dawn were more directed toward the near shore than those at peak migration (Figure 4). At each of the 3 radars, the effect of time on flight direction was significant but the effect of location on flight direction was not significant (Table 4). There were no significant interactions between factors at any of the radars. Birds changed their flight direction at dawn compared to peak migration at each radar, but there was no difference in flight direction over land and over water at either dawn or peak migration.

Differences in Reflectivity for Near and Far Shores

The VIR of migrating birds aloft over water within 3 km of shorelines at dawn was 21% higher at the far shores than at

near shores when data were pooled across all radars (Figure 5). Bird density aloft over land within 3 km of shorelines at flight exodus on subsequent evenings was 48% higher at near shores than at far shores (Figure 5).

There was a significant interaction term ($P < 0.001$, $n = 650$) between time (dawn vs. peak exodus) and shoreline (near vs. far shore) factors, indicating that the effect of near vs. far shore on reflectivity is not the same at dawn and exodus. Based on the results of independent ANOVA tests for dawn and exodus data, the differences in near- and far-shoreline reflectivity at dawn over water were marginally significant ($P = 0.044$, $n = 325$) and the differences at exodus over land between near and far shores were significant ($P < 0.001$, $n = 325$).

The correlation between seasonal mean dawn reflectivity over water and seasonal mean exodus reflectivity over land for pairs of adjacent segments was moderately positive when all shoreline segments were considered together ($r = 0.269$, $P < 0.001$, $n = 325$). When near and far shores were considered separately, the correlation was much stronger for near shores ($r = 0.584$, $P < 0.001$) than for far shores ($r = 0.280$, $P < 0.001$).

DISCUSSION

Migrating birds showed large differences in aggregate flight behaviors between peak nocturnal migration and dawn. These changes were characterized by increased flight height and changes in flight direction that generally resulted in birds orienting themselves toward the near shores of the Great Lakes at dawn. At dawn, birds showed further increases in flight height over water than over land, but this effect was not present during peak migration.

Dawn reorientation of migrating birds aloft toward the nearest shorelines is consistent with other studies that have documented dawn ascent flights (Myres 1964, Diehl et al. 2003, Bowden et al. 2015, Rathbun et al. 2016). Additionally, as morning approaches, nocturnally migrating birds have been found to reorient toward land along the Atlantic coast of the United States (Horton et al. 2016) and along the Mediterranean Sea (Bruderer and Liechti 1998).

TABLE 2. Approximate distance to the horizon for an observer at the mean flight height of migrating birds, at peak nocturnal migration and at dawn, for 3 radars within the Great Lakes region, USA, during spring migration, 2010–2013. Approximate ranges of lake widths within each radar domain are also presented for comparison.

| Parameter | Radar | | |
|---|-------|-------|---------|
| | KCLE | KGRB | KGRR |
| Distance to horizon at mean height of birds at peak nocturnal flight (km) | 93 | 75 | 82 |
| Distance to horizon at mean height of birds at dawn (km) | 92 | 102 | 114 |
| Width of lake (km) | 50–70 | 80–90 | 120–130 |

TABLE 3. Results of an analysis of variance for differences in flight height among groups of migrating birds in the Great Lakes region, USA, during spring migration, 2010–2013. Radar (KCLE, KGRB, KGRR), time (dawn vs. peak migration), and location (land vs. water) were included as grouping factors.

| Source | Sum of squares | df | Mean square | F | Probability > F |
|----------------|----------------|-----|-------------|--------|-----------------|
| Radar | 1,309,990 | 2 | 654,995 | 30.91 | <0.001 |
| Time | 3,708,900 | 1 | 3,708,900 | 175.03 | <0.001 |
| Location | 43,629 | 1 | 43,629 | 2.06 | 0.15 |
| Radar*time | 2,126,251 | 2 | 1,063,125 | 50.17 | <0.001 |
| Radar*location | 109,189 | 2 | 54,593 | 2.58 | 0.078 |
| Time*location | 122,932 | 1 | 122,932 | 5.80 | 0.016 |
| Error | 6,738,344 | 318 | 21,190 | | |
| Total | 15,572,854 | 327 | | | |

The increase in flight height is presumed to be a response by which birds evaluate the width of the ecological barrier posed by the large Great Lakes (Diehl et al. 2003). Migrants over Lake Michigan increased in height at dawn. Migrants increased their flight heights at dawn enough to appear to allow them to see across the lake. Greater increases in heights occurred with a wider lake crossing. This is somewhat consistent with the results of Bruderer and Liechti (1998), who found that birds flying over the widest part of the Mediterranean Sea flew higher than birds crossing near the Iberian Peninsula. However, they could not rule out topographic relief as a factor in these differences and did not observe significant ascent of birds at dawn. Rather, birds flew at the same heights throughout the night. A return to habitat on the near shore may be the result of birds deciding that the crossing is too wide to attempt until the following evening exodus, after flying high enough to see to the other side. We encourage

further investigation of whether birds seek a higher vantage point at dawn to observe the width of a water crossing. It would be interesting to see if a similar response would be observed when the body of water is too wide for migrants to see the other side, even with the increased flight heights associated with dawn ascent.

We estimated that only birds flying over Lake Erie near KCLE were likely able to see across the entire lake during peak nocturnal migration. Interestingly, no increase in flight height at dawn was observed at the KCLE station. It is possible that the narrower crossing presented by Lake Erie eliminates the need to increase height at dawn. However, birds were already flying higher, on average, at the KCLE station during peak migration than at the other sites.

Our finding of a reorientation response is also consistent with birds at dawn seeking stopover habitat on the near shores of the Great Lakes. Diehl et al. (2003) suggested that

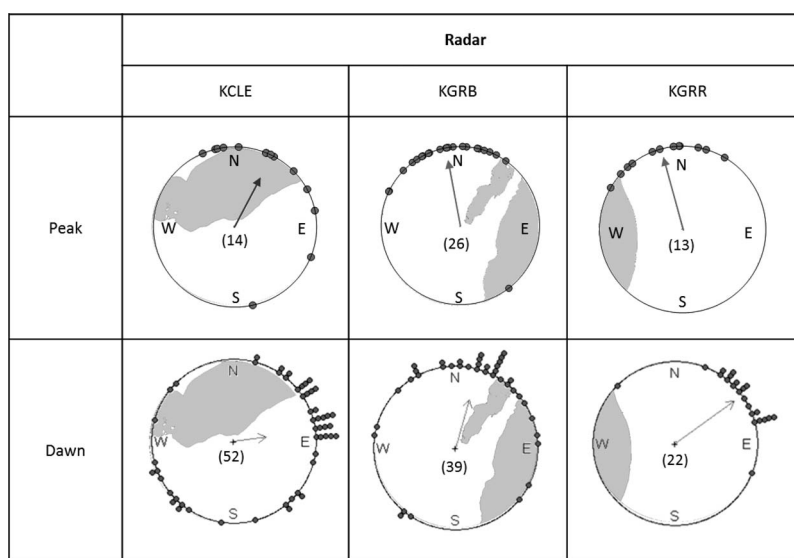
**FIGURE 4.** Circular histograms showing daily mean flight-track directions for birds in the Great Lakes region, USA, at peak migration (i.e. 3 hr after sunset) and at dawn for each NEXRAD radar station, 2010–2013. Sample sizes are given in parentheses. The mean across all years is indicated by an arrow. Dots represent the observed mean direction for an individual day. A map of the land (white) and water (gray) areas within 100 km of the radar station is shown within the circular histograms for reference.

TABLE 4. Results of a Harrison-Kanji test for differences between groups of migrating birds in flight direction at dawn and during peak migration in the Great Lakes region, USA, during spring migration, 2010–2013. Separate tests were done for each radar, including time (dawn vs. peak migration) and location (over water vs. over land) as grouping factors.

| Radar | Factor | df | χ^2 | <i>P</i> |
|-------|-------------|----|----------|----------|
| KCLE | Time | 2 | 16.11898 | <0.001 |
| | Location | 2 | 0.290949 | 0.86 |
| | Interaction | 1 | 0.311419 | 0.58 |
| KGRB | Time | 2 | 10.89632 | 0.004 |
| | Location | 2 | 3.127111 | 0.21 |
| | Interaction | 1 | 2.932581 | 0.087 |
| KGRR | Time | 2 | 76.47924 | <0.001 |
| | Location | 2 | 1.347019 | 0.51 |
| | Interaction | 1 | 1.018962 | 0.31 |

this response may result from evolutionary pressures posed by the difficulty of lengthy crossings across large water bodies. Although the threat of drowning when crossing the Great Lakes is likely minimal in comparison to larger water crossings within North America, such as the Gulf of Mexico, mass mortality of landbirds attempting to cross Lake Michigan can occur (Diehl et al. 2014).

As a consequence of returning to the near shoreline at dawn rather than continuing across to the far shore, migrating birds concentrate at higher densities on near shores than on far shores. This was evidenced by greater VIR of birds emanating from stopover habitats on the near shores for all radars during evening exodus. The correlation between the density of birds over water at dawn and the density of birds at exodus on adjacent shorelines links dawn activity over water and the subsequent distribution of birds in shoreline stopover habitat. The fact that this relationship was much stronger on near shorelines supports the hypothesis that birds that are generally close to shorelines tend to return to stopover habitat on the near shore at dawn rather than continuing across the lake during the day. Unfortunately, low-flying birds could not be detected far from shorelines by the radars we used, so whether most birds far from shorelines also reorient toward shorelines or not is difficult to evaluate. However, Diehl et al.'s (2003) results suggest that reorientation is likely limited to migrants within 28 km of a shoreline. Additionally, lake avoidance by birds altering their course to remain over land along the long axis of the lakes in spring, which seems less common than lake crossing, will also tend to direct more birds along the near shores of lakes (Gauthreaux 1980, Diehl and Larkin 1998, Diehl et al. 2003). Lake avoidance is more apparent in spring than in fall and may contribute to the higher concentrations of migrants on near shores. Finally, an unmeasured subset of migrants may drop out into shoreline stopover habitat during the night, which also contributes to higher densities

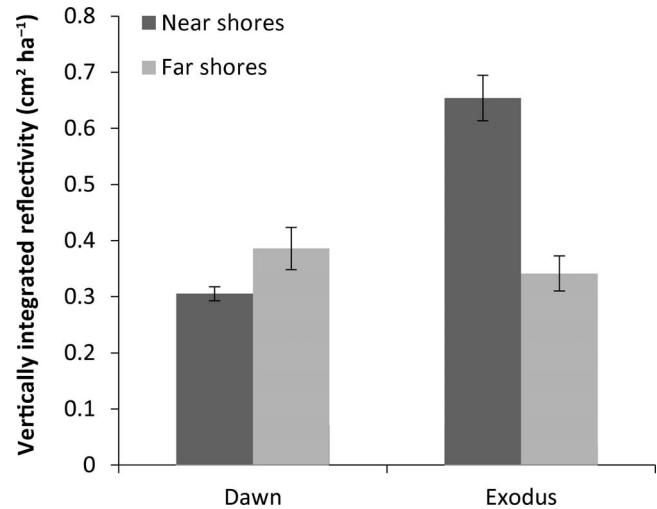


FIGURE 5. Pooled mean values (\pm SE) of vertically integrated reflectivity ($\text{cm}^2 \text{ha}^{-1}$) of migrating birds within 3 km of the shoreline in the Great Lakes region, USA, 2010–2013, for all near and far shores, over water at dawn and over land at exodus.

on the near shore. Dawn ascent is likely one of several behaviors that contribute to the overall importance of the near shore's stopover habitat.

There was no increase in VIR of migrants on near shores compared to far shores at dawn to accompany the large increase observed at exodus. In fact, near shores showed slightly lower VIR over water at dawn than far shores. It is possible that, at dawn, migrants are more likely to drop out into stopover habitat along near shores than on far shores. The increased numbers of birds landing on the near shores of the lake reduced the density of migrants aloft at dawn, despite the general pattern of birds returning to near shores, and contributed to the increased VIR of migrants observed at exodus the following evening. In short, it seems that dawn ascent behaviors in the Great Lakes result in migrating landbirds accumulating in stopover habitat along the near shores of the lakes on the ground, but not in the atmosphere at dawn. We encourage studies using small-scale surveillance radars to better resolve the dynamics of flight behavior as birds approach shorelines and determine how far inland birds travel before making landfall at dawn (e.g., Bowden et al 2015, Rathbun et al. 2016).

The linkage of dawn ascent and reorientation of migrating birds in the Great Lakes with greater shoreline densities of migrants indicates that the stopover habitats on near shores are an important resource for migrating birds. Because the "near shore" of a lake is dependent on the flight direction of the migrating birds, the relative importance of shoreline stopover habitat on northern and southern shores of the Great Lakes is dependent, in part, on the migration season. The dawn flight behaviors of

migrating birds that we report here suggest that habitat on the near shores (i.e. the southern side of Lake Erie and the eastern side of Lake Michigan) is important in spring, whereas habitat on the far shore may be important in fall.

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Author contributions: K.M.A., J.J.B., J.A.S., and R.J.S. conceived the idea and study design and wrote and edited the manuscript. K.M.A., J.J.B., and J.A.S. performed radar data screening and processing. K.M.A. and J.J.B. analyzed the data.

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