Successful migration depends upon finding suitable stopover sites (Degraaf and Rappole 1995, Alerstam 2009, Bayly et al. 2017). The majority of passerines in North America migrate at night, stopping frequently along their migration routes to rest and refuel (Degraaf and Rappole 1995, Alerstam 2009, Paxton et al. 2017, Rushing et al. 2017). Evidence suggesting that much of the annual mortality of several species of passerines occurs during migration (Sillett and Holmes 2002, Rockwell et al. 2016, Paxton et al. 2017, Rushing et al. 2017). The majority of passerines in North America migrate at night, stopping frequently along their migration routes to rest and refuel (Degraaf and Rappole 1995, Alerstam 2009, Bayly et al. 2017). Successful migration depends upon finding suitable stopover sites...
with sufficient food resources to build up fat reserves (Rushing et al. 2017). Mortality during migration may be caused by a variety of natural and anthropogenic sources (Van Doren et al. 2017) including predation, collisions with buildings or other structures (Calvert et al. 2015, Loss et al. 2015), and adverse weather conditions (Butler 2000, Diehl et al. 2014). The latter are predicted to become more frequent with climate change (Torrescano-Valle and Folan 2015, Cohen et al. 2017).

Understanding the migration patterns of birds in relation to landscape configuration and human land uses may help to identify ways to reduce the risks of mortality during migration (Rushing et al. 2016, Smith and Dwyer 2016, Cohen et al. 2017, Reynolds et al. 2017). The airspace where birds migrate can be considered habitat (Diehl 2013) but is rarely considered as such in bird conservation policies (Davy et al. 2017). Understanding how birds use this habitat, i.e., where birds fly through, can inform conservation actions to reduce risks to birds during active migration (Smith and Dwyer 2016). Among others, weather surveillance radars (WSR) have been identified as key tools for region-wide mapping of the distribution of stopover and airspace habitats, including airspace corridors of nocturnal migrants (Kelly and Horton 2016, Bauer et al. 2017, Cohen et al. 2017, Davy et al. 2017, Horton et al. 2019). While weather radars have been used to study some aspects of bird migration such as stopover habitats (Buler and Dawson 2014), or wide-ranging nocturnal flyways (Lafluer et al. 2016, Nilsson et al. 2019), they have more rarely been used for finer scale biogeographical studies.

The behavior of migratory birds at night in relation to coastlines, including the Great Lakes, is of particular interest as many human developments happen along coasts (Buler and Moore 2011, Rosenberg et al. 2016). Flying over open water may be risky and birds may alter their migration paths to reduce time spent flying over these areas, leading to concentrations of birds flying near coastlines. As a consequence, coastal habitats may temporarily shelter high concentrations of birds (Simons et al. 2004). However, where birds do concentrate along coastlines, urbanized areas represent both direct and indirect threats to their survival (Buler and Moore 2011, Rosenberg et al. 2016). For example, nocturnal passerine migrants, including long distance migrants such as warblers, vireos, thrushes, and sparrows account for much of the documented mortality related to collisions with buildings (Loss et al. 2014).

Several previous studies have shown that large water bodies, including the Great Lakes in North America, can influence the way that migrating birds use the airspace (Alerstam 1990, Berthold 1993, Newton 2007, Kranstauber et al. 2015, Weisshaupt et al. 2018). Birds in nocturnal migration encountering coasts perpendicular to their preferred flight direction are likely to continue across the water body, as long as it is not too wide to cross before daybreak (Diehl 2003). In contrast, birds may concentrate along coastlines if they are oriented in the same general direction as their preferred migration direction, especially toward the end of the night (Bruderer and Liechti 1998, Gagnon et al. 2011a, Desholm et al. 2014, Horton et al. 2016a). Funnel-shaped geography may act as a bottleneck, concentrating migratory birds (La Sorte et al. 2016, Baily et al. 2017), with the degree of concentration proportional to the size of the terrestrial landscape drained (Gagnon et al. 2011a, Desholm et al. 2014). The size and complex configuration of the Great Lakes (shape and orientation of coastlines) surrounding southern Ontario, Canada, suggest they are likely to influence nocturnal migration of birds. However, analyses of flight patterns of nocturnal migrants have mainly focused on areas in the United States, mostly south of the lakes (e.g., Farnsworth et al. 2016, Horton et al. 2016b, Heist et al. 2018), other than one study of diurnal migrants on the U.S. portion of the north shore of Lake Superior (Peterson et al. 2015).

The objectives of our study were to determine how the nocturnal migration patterns of birds in southern Ontario are influenced by the three Great Lakes surrounding this area (Lake Huron, Lake Erie, and Lake Ontario) using Canadian weather surveillance radars (CWSR). More precisely, we evaluated whether bird concentrations in the airspace and their migratory orientation were affected by near-scale (about 10–30 km) or broader-scale (> 150 km) landscape features of the Great Lakes. Our hypotheses were: 1) the Great Lakes shape the nocturnal passerine migration in southern Ontario in terms of flight direction and bird density; 2) the effect of the Great Lakes on flight direction and bird density is more pronounced near coastlines oriented at acute angles to the general preferred flight direction; and 3) the effect is more pronounced later at night when birds may be more reluctant to cross the lakes. Understanding migration patterns and use of airspace in southern Ontario is a pressing issue for bird conservation as this region is a densely populated area, with increasing development posing many potential threats to migrating birds (Calvert et al. 2013).

METHODS

Study area and radar data

We examined nocturnal bird migration in southern Ontario, Canada, in an area bordered by three of the Great Lakes: Lake Ontario, Lake Erie, and Lake Huron. This area is within range of two CWSR used in this study, namely King City (WKR) and Exeter (WSO; Fig. 1, 2, and 3). More details on the technical characteristics of the radars and the radar data analysis are presented in Appendix 1.

We used radar data for three consecutive years (2009–2011) covering autumn migration from August 15 to October 29, and for two consecutive years (2010–2011) covering spring migration from April 15 to May 26. These years were selected at the time the study was designed and data ordered (2012), although the study took several years to complete.

Birds are most reliably detected with these radars within 60 km, so for our main analyses, we used only data within 60 km of the radar, although under some conditions birds can be detected at 80 km, so we included some supplementary data from that distance.

We initially selected nights for analysis if wind conditions were favorable for heavy migration. We focused on nights with strong migration for two reasons. First, these represent the nights when the vast majority of individuals migrate. Second, the C-band CWSR used in this study had peak power of 250 MW (substantially less than the 1000 MW for the U.S. S-band weather radars), and hence was less able to detect birds when there were few individuals migrating. We considered winds favorable in autumn when they were light to moderate with a northerly component or light from any direction; and in spring when they...
Fig. 1. Median flight directions of nocturnal migration in southern Ontario, Canada, in (A) autumn (years 2009–2011) and (B) spring (years 2010–2011), measured with two Canadian weather surveillance radars, namely King City (WKR) and Exeter (WSO). Arrows are circular medians of the nightly flight directions at 2.5 h (black bold) and 6 h after sunset (thin blue; not visible when under black arrow) at 20, 40, and 60 km of range along four azimuthal points: 1) maximum negative velocity (where birds are coming straight forward on the radar); 2) and 3) zero velocity left and right of maximum positive velocity (where birds move tangentially to the radar), and 4) maximum positive velocity (where birds are flying straight away from the radar. The numerical angle beside each pair of arrows is the mean change of flight directions between times for nights having data at both times; an asterisk beside a blue arrow indicates a significant change of flight direction late at night compared to early night (see Methods and Appendix 1 for more details). Note that the mean change of flight direction may differ from the angle between the arrows on the map, because the arrows represent all available data, including nights of missing data at either time. Note that the maps of flight directions and bird densities should only be interpreted in conjunction with the tables and text, due to differences in apparent RCS of birds at different locations and different time periods on the maps.

were light to moderate with a southerly component, following Richardson (1978, 1990) and Gagnon et al. (2011b). We used data on wind conditions aloft taken from atmospheric soundings at the Detroit (DTX) and Buffalo (BUF) weather stations (http://weather.uwyo.edu/upperair/naconf.html) at 00h00 UTC to determine which nights to examine. We subsequently excluded time periods when the radar images indicated significant precipitation within the study areas. As a result, the number of nights analyzed varied among years, seasons, and radars due to differences in weather conditions. We further excluded nights when little (short range of detection [< 50 km]) or no migration was detected at a particular radar. In total, we analyzed 54 and 50 nights over 3 years in autumn, and 19 and 28 nights over 2 years in spring for the WKR and WSO radars, respectively.

Estimating flight direction

We estimated flight directions by visualizing the velocity azimuth display (VAD) in the software RAPID which uses Doppler information to indicate movement in relation to the radar (Appendix 1). Flight directions were measured twice per night, at 2.5 h and 6 h after sunset, representing peak activity early and later in the night, when most birds are likely to be in active migration, rather than taking off or landing (Gagnon et al. 2011a). There are four azimuthal points around the radar that provide reliable estimates of flight directions: 1) the direction of maximum negative velocity, where the targets are flying straight toward the radar (approximately north of each radar in fall, south in spring); 2) the direction of maximum positive velocity, where the targets are flying directly away from the radar (approximately south of each radar in fall, north in spring); 3) and 4) the directions of zero velocity to the left and right of maximum positive velocity, where the targets are flying tangentially to the radar. The flight direction is determined at each azimuthal point as follows: at maximum positive velocity, the flight direction is simply the azimuth at the maximum value; at zero velocity to the left and right of maximum positive velocity, where the targets are flying tangentially to the radar. The flight direction is determined at each azimuthal point as follows: at maximum positive velocity, the flight direction is simply the azimuth at the maximum value; at zero velocity to the right of the maximum
Fig. 2. Indices of density of nocturnal passerine migrants in autumn in southern Ontario, Canada, sampled in groups of blocks around WKR and WSO weather radars, over three years (2009–2011) at (A) 2.5 h and (B) 6 h after sunset. Group ID’s are followed by sample sizes (n) in terms of number of nights. Scale of bird densities η (the total surface area of birds by volume of atmosphere [cm²/km³]) in blocks is the same for the two maps. Letters appearing beside blocks are results of Tukey pairwise comparison between blocks within group using the best fit LMM or GLMM models, where blocks having no letter in common are significantly different from the others (α ≤ 0.05) and where in B) an asterisk beside a block indicates a significantly different bird density at 6 h after sunset compared to 2.5 h after sunset. The true block size is 3° x 3 km, but for the graphic is enlarged to 5° x 5 km to make it easier to see. Dashed circles around radars indicate the 40 km radar range. See Methods and Appendix 1 for more details. Note that densities depicted by color coding in Figures 2 and 3 are standardized for comparison within groups, but can not be compared reliably among groups, as they do not include all the same nights and also birds present different aspects given the angle of view, and hence different reflectivity per bird.
Fig. 3. Spring densities of nocturnal passerine migrants (\( \eta \)) in southern Ontario, Canada, sampled in groups of blocks around WKR and WSO, over two years (2010–2011), at 2.5 h (A) and 6 h (B) after sunset. The scale, legend, and limitations in interpretation are the same as in Figure 2.
velocity, the flight direction is the azimuth-90°; and at zero velocity to the left of the maximum velocity, the flight direction is the azimuth-270°. Values were transposed to positive values on the 0–360° compass where 0° is due north. If sufficient bird activity was detected, we estimated flight direction at each of these four azimuthal points at 20, 40, 60, and 80 km from the radar, representing altitudes of about 85–312, 216–670, 395–1076, and 622–1529 m above ground, given the scanning angle of 0.5° and normal propagation conditions. At WSO, we also sampled birds at 30 km from the radar on the west side to estimate activity along the Lake Huron shoreline. Migration was only rarely detected beyond the 60 km range, so we present the 80 km data only in Appendix 3. Data on flight directions were estimated for the same dates as we estimated bird densities if sufficient data were available to estimate reliable flight directions.

**Estimating bird density**

We sampled bird densities at the same times as we estimated flight direction, at 2.5 h and 6 h after sunset for all nights when visual examination of the data and computation of the target’s airspeed suggested measurable bird migration. We estimated the relative density of nocturnal bird migrants using radar reflectivity (dBZ), assuming that most reflectivity was due to birds, although recognizing that additional biological targets (insects and bats) may account for some unknown proportion of the reflectivity. Using the URP software, measurements of reflectivity were automatically extracted from all cells within a series of sampling blocks of 3 km in radial length by 3° of azimuthal width (Fig. 2). The value of reflectivity inside a sampling block is the mean of Z (linear reflectivity) of all cells in the block, after filtering out unwanted non-biological echoes (Appendix 1).

We estimated an index of bird density within each block as the total radar cross-section (RCS) of targets by volume of atmosphere (cm$^2$km$^{-3}$) using the equation of Chilson et al. (2012) to convert Z to the linear unit $\eta$. Dokter et al. (2018a), based on Dokter et al. (2011), estimated the total number of individual birds around a radar by dividing $\eta$ over all azimuths by an averaged RCS of 11 cm$^2$. However, the relationship between $\eta$ and the actual number of birds is complex for several reasons. First, although most migrants are assumed to be passerines, the species composition and size distribution is unknown. Second, the relationship between a bird’s body cross-section and RCS is non-linear, because most passerines fall within the Mie scattering region, where, for example, small birds such as warblers may sometimes have a higher RCS than some larger birds such as thrushes (Alerstam 1990). Furthermore, the RCS also varies with the angle of view (e.g., head, side, and tail views), meaning that birds flying perpendicular to the radar tend to have a higher RCS than birds flying toward or away from the radar (Edwards and Houghton 1959, Houghton 1969). Thus, use of average RCS could produce quite misleading results for finer scale analyses of densities at different positions within a radar coverage.

To control for variation of RCS caused by variation in the angle of the birds, we based our statistical comparisons on groups of blocks selected to test specific hypotheses (Fig. 2 and 3). Around each radar, we selected blocks clustered in 5 groups of 4 to 5 blocks each. Within each group, all blocks were at the same radar range (varying from 36.5 to 51.5 km from the radar depending on the group) and within an azimuthal window of 30°, except group 10 which had 5 blocks spread across 39°. We assumed that within this narrow azimuthal window, most variations in RCS among blocks were due to variation in bird density rather than variation in the body orientation of the birds in relation to the radar. We also assumed that differences between paired groups reflected differences in bird densities if both groups were at a similar angle in relation to the main axis of bird movement, but on opposite sides (i.e., to the east or west of the axis of migration).

**Statistical analysis**

**Analysis of flight directions**

For each season and time of night, we calculated the circular median flight direction across all nights with adequate data at each of the four azimuthal points and each of the radar ranges. We calculated the circular mean of the within-night changes of flight direction at 6 h after sunset as compared to 2.5 h for all possible paired samples for each of the 12 azimuthal points, and we then computed the 95% confidence intervals (CI) of these means. More details on our circular data analysis are given in Appendix 2.

**Raw nightly observations of flight directions**

We also used the raw nightly observations of flight directions measured at a 40 km range as they revealed some patterns in flight behavior that were not shown by a central statistic, such as the median. We present these data in circular plots separately for each radar and each season, at the four azimuthal points, to show the distribution and variation in flight patterns among nights. For ease of explanation, we refer to these azimuthal points using the approximate cardinal directions, but note that the actual locations of the measurements vary depending on the flight direction of the birds.

**Circular statistics summaries on flight directions**

To test whether the nightly observations of flight directions at the four azimuthal points at 40 km from each radar had similar distributions within each radar and time, we calculated summary circular statistics and compared them using paired-sample tests. We computed the median and the mean deviation for the median, the skewness, and the kurtosis along with their 95% CIs.

**Comparing bird density between radars**

We compared average bird density between the radars to test for differences between the east and west of the study area. At this scale, we combined data from all blocks, because the groups of blocks were distributed roughly equally around both radars, thus giving an overall average, as has been done in some other WSR studies (Dokter et al. 2011, Dokter et al. 2018a). The sets of blocks at both radars cover roughly the same intervals of altitudes, as they are a similar distance from each radar (at a 40 km range, under normal propagation conditions these cover approximately 576–1030 m asl (above sea level) for WKR and 519–973 m asl for WSO). We calculated the mean bird density $\eta$ at each radar, night, and time. More details are given in Appendix 2 on statistical analysis of these data.

**Comparison of bird density within groups of blocks**

We compared bird density among blocks within each group to test whether densities varied over relatively short distances in relation to factors such as coastlines. We used LMM or GLMM, fitted separately by season and by radar to model bird density $\eta$
Table 1. Comparing bird densities between radars in (A) autumn (2009–2011) and (B) spring (2010–2011). Rows at time 2.5 and 6 h after sunset within each season present the number of nights compared (n), the estimated mean bird densities index (\( \eta \pm SE \)) at WSO and WKR weather radars, with the mean ratios of bird densities \( \eta \) between WKR and WSO (± SE), the t-ratio and the p-values from statistical contrasts between radar using valid weighted linear mixed models (see Appendix 1). Columns of WSO and WKR present the comparison of bird densities between times within each radar separately, with the mean bird densities ratios between times (± SE), followed by the t-ratio and the p-value from statistical contrasts between times using the same former models.

| Season | Time (hours) | n | WKR (\( \eta \pm SE \)) | WSO (\( \eta \pm SE \)) | Ratio (WKR/WSO ± SE) | t-ratio | p-value |
|--------|-------------|---|------------------------|------------------------|----------------------|--------|--------|
| A) Autumn | 2.5 | 31 | 519 ± 57.3 | 337 ± 37.5 | 1.54 ± 0.047 | 14.195 | < 0.001 |
| | 6 | 27 | 306 ± 34.0 | 172 ± 19.2 | 1.78 ± 0.058 | 17.717 | < 0.001 |
| ratio (6/2.5 ± SE) | | | 0.59 ± 0.017 | 0.51 ± 0.018 | | | |
| | t.ratio | | -18.789 | -18.696 | | | |
| | p.value | | < 0.001 | < 0.001 | | | |
| B) Spring | 2.5 | 12 | 245 ± 43.7 | 104 ± 18.5 | 2.35 ± 0.109 | 18.447 | < 0.001 |
| | 6 | 9 | 171 ± 30.7 | 89 ± 16.0 | 1.91 ± 0.099 | 12.461 | < 0.001 |
| ratio (6/2.5 ± SE) | | | 0.70 ± 0.038 | 0.86 ± 0.047 | | | |
| | t.ratio | | -6.635 | -7.279 | | | |
| | p.value | | < 0.001 | 0.011 | | | |

RESULTS

Autumn migration

Regional patterns

In autumn, the density of birds aloft in the eastern half of the study area, averaged across all plots around WKR, was estimated to be 1.54 to 1.78 times higher than the average of plots to the west around WSO, at 2.5 h and 6 h after sunset, respectively (Table 1A). This suggests a concentration of birds between Lake Ontario and Georgian Bay. As the night progressed, bird density aloft decreased significantly, with densities at 6 h after sunset averaging 0.51 to 0.59 times those measured at 2.5 h after sunset at WSO and WKR, respectively (Table 1, Fig. 2).

Overall, flight directions were S to SSW at both radars early in the evening, but with a tendency to be slightly more southerly at WKR. As the night progressed, migration shifted to a more SW direction, suggesting greater avoidance of directions that head directly toward Lake Ontario or Lake Erie later in the night (Fig. 1A, 4).

Patterns near Georgian Bay

North of WKR, at both 2.5 h and 6 h after sunset, flight directions were highly concentrated toward S (Fig. 4A, Table 2A, 2B). There was a significantly greater density of birds at the easternmost block of group 4 located straight south of the eastern extremity of Georgian Bay than the more western blocks, 2.5 h after sunset (Fig. 2A), suggesting a concentration of birds that had flown around Georgian Bay. In addition, there were 1.62 and 1.35 more migrants in group 4 as compared to group 5 at 2.5 h and 6 h, respectively, after sunset on nights when migration was predominantly southward (Table 3A), indicating fewer birds migrating east and inland from Georgian Bay (Fig. 2).

Patterns near Lake Ontario

East of WKR, 2.5 h after sunset, autumn flight directions varied considerably among nights as indicated by low concentration values and a relatively flat distribution (low kurtosis; Table 2A). Overall, there was a bimodal pattern with peaks to SSE and SW...
Fig. 4. Nightly flight directions of nocturnal migrants observed around WKR and WSO in (A to H) autumn (2009–2011) and (I to P) spring (2010–2011), at each of the four azimuthal points around the radars named based on the approximate cardinal location relative to the radar (as described in Methods), measured at 40 km of range (except at 30 km ~ west of WSO). Graphs show nightly observations of flight directions (dots), circular median (arrows) and circular densities (lines) for two times: 2.5 h (outer filled points, black bold arrow and line) and 6 h after sunset (inner open points, blue thin arrow and line). The circles are divided in 36 bins of 10 degrees for both nightly observations and circular densities. Statistical summaries of these data are presented in Table 2.
Table 2. Circular statistics summaries of the flight directions measured in (A to D) autumn (years 2009–2011) and (E to H) spring (years 2010–2011), around WKR and WSO weather radars in southern Ontario, Canada, at 2.5 and 6 h after sunset. Data are from each of the four azimuthal points at 40 km range, with approximation (~) of the cardinal location relative to the radar and the reference between brackets to sub-figures of Figure 4, where the number of observations (n) are followed by statistics on distribution. Statistics include: median, skewness, and kurtosis with their spread in parentheses, and where statistical tests on common median and common distribution present azimuthal points members of the same statistical group when sharing the same letter within season, radar, and time.

| Season | Radar | Time (hour) | Azimuthal point (cardinal [refers to Fig.4]) | n  | Median | Common median | Skewness | Kurtosis | Common distribution |
|--------|-------|-------------|-----------------------------------------------|----|---------|----------------|----------|----------|---------------------|
| A) Autumn | WKR  | 2.5 | Max Negative (~North [A]) Zero Left (~East [B]) Max Positive (~South [C]) Max Right (~West [D]) | 44 | 187° (166, 208) | a | 0.002 (0.081, 0.085) | 0.686 (0.557, 0.816) | a |
|         |       |       |      | 42 | 190° (159, 221) | ab | 0.041 (-0.054, 0.136) | 0.456 (0.329, 0.583) | b |
|         |       |       |      | 47 | 201° (172, 230) | b | -0.095 (-0.249, 0.059) | 0.561 (0.396, 0.726) | b |
|         |       |       |      | 41 | 193° (167, 219) | ab | 0.036 (-0.070, 0.141) | 0.593 (0.442, 0.744) | ab |
| B) Autumn | WKR  | 6   | Max Negative (~North [A]) Zero Left (~East [B]) Max Positive (~South [C]) Max Right (~West [D]) | 37 | 190° (164, 216) | ab | 0.095 (0.024, 0.165) | 0.486 (0.288, 0.683) | a |
|         |       |       |      | 36 | 201° (174, 229) | ab | -0.073 (-0.190, 0.043) | 0.523 (0.377, 0.670) | ab |
|         |       |       |      | 41 | 204° (179, 229) | b | -0.129 (-0.260, 0.003) | 0.613 (0.442, 0.785) | b |
|         |       |       |      | 35 | 189° (163, 215) | a | 0.051 (-0.035, 0.136) | 0.613 (0.456, 0.770) | a |
| C) Autumn | WSO  | 2.5 | Max Negative (~North [E]) Zero Left (~East [F]) Max Positive (~South [G]) Max Right (~West [H]) | 44 | 199° (181, 218) | a | 0.081 (0.022, 0.141) | 0.695 (0.553, 0.836) | a |
|         |       |       |      | 42 | 201° (171, 231) | a | 0.060 (-0.043, 0.162) | 0.418 (0.257, 0.579) | b |
|         |       |       |      | 40 | 202° (186, 218) | a | 0.005 (-0.029, 0.038) | 0.744 (0.636, 0.852) | a |
|         |       |       |      | 45 | 200° (180, 220) | a | 0.120 (0.043, 0.197) | 0.652 (0.484, 0.820) | a |
| D) Autumn | WSO  | 6   | Max Negative (~North [E]) Zero Left (~East [F]) Max Positive (~South [G]) Max Right (~West [H]) | 39 | 209° (177, 241) | a | 0.079 (-0.020, 0.178) | 0.434 (0.290, 0.577) | ab |
|         |       |       |      | 39 | 224° (190, 258) | a | 0.015 (-0.103, 0.134) | 0.393 (0.272, 0.515) | a |
|         |       |       |      | 37 | 213° (193, 233) | a | -0.007 (-0.039, 0.025) | 0.675 (0.569, 0.780) | b |
|         |       |       |      | 41 | 204° (166, 242) | a | 0.140 (0.025, 0.255) | 0.303 (0.096, 0.511) | a |
| E) Spring | WKR  | 2.5 | Max Positive (~North [I]) Zero Right (~East [J]) Max Negative (~South [K]) Max Right (~West [L]) | 17 | 21° (355, 47) | ab | -0.015 (-0.111, 0.080) | 0.488 (0.270, 0.707) | ab |
|         |       |       |      | 17 | 36° (16, 56) | c | -0.153 (-0.294, -0.011) | 0.619 (0.319, 0.920) | a |
|         |       |       |      | 17 | 26° (9, 43) | a | -0.078 (-0.152, -0.005) | 0.698 (0.487, 0.909) | ab |
|         |       |       |      | 16 | 12° (348, 35) | b | -0.109 (-0.178, -0.039) | 0.555 (0.294, 0.815) | b |
| F) Spring | WKR  | 6   | Max Positive (~North [I]) Zero Right (~East [J]) Max Negative (~South [K]) Max Right (~West [L]) | 16 | 9° (346, 32) | a | 0.037 (-0.039, 0.114) | 0.588 (0.374, 0.802) | a |
|         |       |       |      | 13 | 9° (355, 23) | a | -0.013 (-0.044, 0.019) | 0.778 (0.628, 0.927) | a |
|         |       |       |      | 15 | 16° (352, 40) | a | -0.195 (-0.296, -0.095) | 0.493 (0.103, 0.883) | a |
|         |       |       |      | 10 | 16° (348, 45) | a | -0.228 (-0.608, 0.152) | 0.561 (0.145, 0.976) | a |
| G) Spring | WSO  | 2.5 | Max Positive (~North [M]) Zero Right (~East [N]) Max Negative (~South [O]) Max Right (~West [P]) | 24 | 19° (0, 38) | a | 0.043 (-0.029, 0.114) | 0.685 (0.509, 0.862) | a |
|         |       |       |      | 22 | 28° (2, 53) | ab | 0.017 (-0.063, 0.097) | 0.484 (0.253, 0.715) | ab |
|         |       |       |      | 24 | 34° (18, 50) | b | -0.040 (-0.157, 0.077) | 0.753 (0.565, 0.941) | b |
|         |       |       |      | 19 | 18° (354, 42) | a | 0.106 (0.019, 0.192) | 0.529 (0.241, 0.818) | a |
| H) Spring | WSO  | 6   | Max Positive (~North [M]) Zero Right (~East [N]) Max Negative (~South [O]) Max Right (~West [P]) | 21 | 32° (12, 52) | a | -0.006 (-0.044, 0.033) | 0.692 (0.558, 0.826) | a |
|         |       |       |      | 19 | 45° (18, 72) | a | -0.056 (-0.141, 0.029) | 0.452 (0.215, 0.689) | a |
|         |       |       |      | 20 | 33° (12, 54) | a | -0.012 (-0.079, 0.054) | 0.611 (0.403, 0.818) | a |
|         |       |       |      | 20 | 30° (10, 50) | a | 0.003 (-0.044, 0.050) | 0.678 (0.529, 0.828) | a |
Patterns near Lake Huron

Autumn flight directions near Lake Huron, around WSO, were predominantly S to SSW, similar to those elsewhere in the region, shifting more to SW later in the night (Fig. 1, Fig. 4E to H, and Fig. A3.1). However, to the W and N of WSO near the coast of Lake Huron (Fig. 4E and H), flight directions were highly skewed (Table 2C and D). Although most nights had flight directions predominantly S to SSW, even well over the lake, there were some nights with directions SW or W heading across Lake Huron, but almost none heading at all E, suggesting few birds arriving from Lake Huron.

Densities in blocks close to Lake Huron were substantially lower than those farther inland for many paired-groups comparisons (Table 3B, Fig. 2). Comparing only nights when the migration direction was centered between groups of blocks, bird densities varied from 1.59 to 4.35 times higher in the inland (eastern) groups both early and later in the night (Table 3B). Within-group bird densities were similar among all blocks of group 1 (E of WKR and WSO weather radars. Paired-groups refers to the group ID compared (locations, Figure 2 or 3) and ordered West-East (ex.: 3:1 means the West group 3 is compared to the East group 1) at time 2.5 or 6 h after sunset, with the number of comparison (n, in number of nights). The flight direction of birds refers to the azimuth approximately at mid-way between the two groups compared (i.e. groups symmetrically opposed). The estimated mean of bird density index ($\eta \pm SE$) is given for the West group and the East group, followed by the ratio of bird densities between East and West ($\pm SE$), and then the z-ratio and p-values from statistical contrasts between groups using valid GLMMs (details in Methods and Appendix 1), where p-value < 0.05 indicates evidence of difference of birds densities between groups, or marginally if 0.05 < p > 0.1.

Table 3. Comparisons of bird densities between paired-groups in (A to B) autumn (2009–2011) and (C to D) spring (2010–2011) around WKR and WSO weather radars. Paired-groups refers to the group ID compared (locations, Figure 2 or 3) and ordered West-East (ex.: 3:1 means the West group 3 is compared to the East group 1) at time 2.5 or 6 h after sunset, with the number of comparison (n, in number of nights). The flight direction of birds refers to the azimuth approximately at mid-way between the two groups compared (i.e. groups symmetrically opposed). The estimated mean of bird density index ($\eta \pm SE$) is given for the West group and the East group, followed by the ratio of bird densities between East and West ($\pm SE$), and then the z-ratio and p-values from statistical contrasts between groups using valid GLMMs (details in Methods and Appendix 1), where p-value < 0.05 indicates evidence of difference of birds densities between groups, or marginally if 0.05 < p > 0.1.
densities also showed significantly higher densities in blocks over the shore or near the coastline as compared to the farthest block over water, at both times of the night (Fig. 2, groups 9 and 10).

**Patterns approaching Lake Erie**

East of WSO, flight directions were distinctly bimodal with some nights showing predominantly S, suggesting a likely direct crossing of Lake Erie, and others predominantly SW. The pattern was similar 2.5 h after sunset and 6 h after sunset, though with more birds heading SW or WSW later in the night (Fig. 4F, Table 2C). South of WSO, flight directions were most frequently SSW toward Rondeau and Point Pelee early in the evening, while later at night they were mostly SW (Fig. 4A, 1G, Table 2C and 2D). There were no significant differences among blocks within any of the inland groups (Fig. 2, groups 6, 7, and 8).

**Spring migration**

**Regional patterns**

In spring, bird density in the east, around WKR, was estimated to be 2.35 to 1.91 times as high as density in the west, around WSO, at 2.5 h and 6 h after sunset, respectively (Table 1B, Fig. 3), suggesting a similar pattern of higher concentration of birds between Lake Ontario and Georgian Bay as was found in autumn. As the night progressed, bird density aloft decreased significantly, though less than in autumn, at both radars, with bird density at 6 h after sunset averaging 0.86 and 0.70 times that measured at 2.5 h after sunset, at WSO and WKR, respectively (Table 1B, Fig. 3).

Flight directions were generally from the NNE to NE at both radars, though with a tendency to be more to the N around WKR after birds had passed the latitude of southern Lake Ontario, and more NE at WSO (Fig. 1B). At both radars, there was some tendency to shift to a more easterly direction as the night progressed, particularly N of WSO, suggesting greater avoidance of directions that head toward Georgian Bay.

**Patterns near Georgian Bay**

North of WKR, spring flight directions varied among nights, from NW to NE at 2.5 h after sunset, with a tendency to become more N at 6 h after sunset (Fig. 4I). Within group 4, significantly more birds passed over the easternmost block compared to the more western blocks, at both times of night; however, there was little variation in densities among blocks within group 5 (Fig. 3). There were too few nights with a due N migration, between groups 4 and 5 to compare densities between these groups.

**Patterns near Lake Ontario**

East of WKR, nocturnal migrants in spring tended to fly NE early at night (Fig. 4J), suggesting they were following the shoreline of Lake Ontario. Later at night, flight directions were more to the N, suggesting predominantly migrants that had crossed Lake Ontario. South of WKR (Fig. 4K) a similar pattern was found, though flight directions were slightly less E.

Along the western edge of Lake Ontario in group 2, bird densities were significantly higher over land and near the shoreline compared to farther offshore (Fig. 3A), while later at night, the highest density was over water within 8 km of the coast (Fig. 3B). In contrast, there were no detectable differences in densities among blocks within group 1 near or away from the shoreline of Lake Ontario. On nights when flight directions averaged 33°, there were no detectable differences in bird density between a rural inland location west of Toronto (group 3) and the western end of Lake Ontario (group 2; Table 3C).

**Patterns near Lake Huron**

North of WSO, spring flight directions varied from N to NE at 2.5 h after sunset, which would bring migrants toward Georgian Bay; while 6 h after sunset, flight directions were more NE which would bring them toward or around the southeast end of Georgian Bay (Fig. 1B, Fig. 4M, Table 2G–H). West of WSO, 2.5 h after sunset, migrants tended to fly N on many nights, suggesting they followed the eastern shoreline of Lake Huron, while on a smaller number of nights they flew E or NE suggesting arrival from crossing the southern end of the lake (Fig. 4P). Later in the night an increasing proportion was flying E or NE (Fig. 4P, Table 2G).

South of WSO, the median direction was about NE (i.e., ~35°) at both times of the night (Fig. 1B, 4O, Table 2G–H), consistent with having come from the W edge of Lake Erie.

No significant variation was detected among blocks within any of the groups around WSO either early or late in the night (Fig. 3). However, on nights when migrants flew NNE (28–31°), allowing comparison of group 10 with group 6, there were 1.66 to 2.88 times more migrants passing about 40 km east of WSO (group 6) at 2.5 h and 6 h after sunset, respectively, as compared to the eastern coast of Lake Huron (Table 3D, group 10), although there were no detectable differences between group 7 and group 9. In contrast, when migration was predominantly 39–43°, there were 1.96 to 2.38 more migrants in group 9 compared with group 8 at 2.5 h and 6 h after sunset, respectively (Table 3D), indicating flight directions were close to the coastline orientation with a concentration of migrants along the southern edge of Lake Huron.

**Patterns near Lake Erie**

At the 40 km range, E of WSO, flight directions varied among nights from N to E, (Fig. 4N, Table 2G–H), suggesting arrival from crossing Lake Erie on some nights, or arrival from SW Ontario on other nights. At 40 km S of WSO, the early-night median flight direction was significantly more NE compared to N of WSO (Fig. 1B, 4O compared to 4M, Table 2G), suggesting most birds had come from SW Ontario, which suggests avoiding crossing Lake Huron.

**DISCUSSION**

Using CWSR, we found that in southern Ontario, the Great Lakes shape the nocturnal migration of birds in autumn and spring, influencing flight directions, and bird density. We found that flight directions in autumn were generally south-southwestward throughout the study area, with many birds passing between Georgian Bay and Lake Ontario thus maximizing flight overland prior to crossing Lake Erie. Nevertheless, there were some nights when migration was more southerly, suggesting extensive lake crossing. In spring, migration was predominantly to the northeast in the western portion of our study area, which aligned migrants roughly between Georgian Bay and Lake Ontario, while migration was more northerly in the eastern portion, still suggesting the previously mentioned alignment.
Effect of the Great Lakes in autumn

Although on some nights many birds do fly over the Great Lakes, we found evidence that densities of birds differed on either side of a line that can be drawn (Fig. 1) from the southern extremity of Georgian Bay to the southern end of the main basin of Lake Huron. On most nights, birds were concentrated along a flyway to the south and east of this line, with the area of lowest bird densities to the north and west of this line. Within this flyway, the densest concentrations were in the east of southern Ontario, passing between Lake Ontario and Georgian Bay, as indicated by the greater densities around WKR compared to WSO. Densities to the south of WSO were up to four times higher than farther N and W, as indicated by comparisons of paired groups around WSO. Birds following this route are on a path to either cross the western half of Lake Erie or else fly around the lake; however, these areas are not well covered by CWSRs, so the locations where birds crossed could not be confirmed.

In autumn, Georgian Bay and Lake Ontario appeared to be the principal water bodies shaping the flyway. The northeast coast of Georgian Bay is oriented approximately SSE (147°), which may be close enough to a southward direction to encourage many birds to follow the coast instead of making an overwater flight of about 80 to 100 km over the bay. Several previous studies of the effects of coastlines on night migrants have found that acute angles between the coastline and the flight direction increase the propensity of birds to follow the coastline (Bruderer and Liechti 1998, Gagnon et al. 2011a, Desholm et al. 2014, Horton et al. 2016a). Preliminary observations of data from the WBI radar at Britt, Ontario, on the north coast of Georgian Bay (F. Gagnon, unpublished observations) indicated that in autumn, immediately after dusk, many birds flew directly south across the bay, but as the evening progressed birds shifted to fly SSE parallel to the north shore of the bay. Furthermore, observations of animated radar images from WKR indicate that many birds departed at dusk from areas at the southeastern extremity of Georgian Bay, mostly from the north shore, suggesting a concentration of birds stopping over in that area (F. Gagnon, unpublished observations). Most of these birds had passed WKR by 2.5 h after dusk, as reflected in the higher concentrations in group 3 (Fig. 2). The tendency for birds to migrate SSW or SW in our study area may indicate some level of compensation after traveling SSE around Georgian Bay.

Lake Ontario also appeared to influence autumn flight directions, but the influence depended on the specific orientation of the coastline. The western quarter of the lake has the shoreline oriented approximately SW for about 80 km, which is close to the preferred flight direction of the birds and appeared to result in many birds following parallel to the coast. This is supported by the higher concentrations of birds over land than over water in this area (Fig. 2, group 2). A previous study (Rathbun et al. 2016) using marine radars, found that the orientation of the southern coastline of Lake Ontario appeared to influence migratory directions as far as 35 km from the coast. However, the central section of the north coast of Lake Ontario is oriented in a more E–W direction (about 260°) which is approximately perpendicular to a southward flight direction. Diehl (2003) suggested birds may be more likely to cross a large water body if the coastline is perpendicular to the preferred direction of travel. This is supported by observations of similar densities of birds in all blocks of group 1 (Fig. 2) suggesting many birds in that area flew directly across the lake.

We did not have observations close enough to Lake Erie to determine its effect on migration orientation, but in an exploratory study with the U.S. WSR of Cleveland (KCLE) over 25 nights in autumn 2010, Gagnon (unpublished data) found evidence of coast-following flights on certain nights along the north coast of the western end of Lake Erie. Many birds appeared to cross the lake at Point Pelee and to a lesser extent at Rondeau, both of which are peninsulas oriented southwards across the lake (Fig. 1).

Overall, these patterns are consistent with a balance between minimizing risks of overwater flights and minimizing costs of detours as suggested by optimal migration theory (Alerstam 2011).

Effect of the Great Lakes in spring

We also found evidence of a concentration area (flyway) in spring, with densities of birds around WKR 1.9 to 2.3 times higher than around WSO. However, this area of concentration appeared to cover a smaller area than in autumn, with highest bird densities to the east of a line between the south of Georgian Bay and the middle of Lake Erie. This pattern is consistent with most birds crossing Lake Erie at some point, rather than flying around it to the west. Some birds flying north across the eastern end of Lake Erie may also cross the western end of Lake Ontario. In spring, if birds cross Lake Erie over its western half, the optimal route overland would be mainly NE; if they cross over the eastern half, the optimal route overland would be mainly NNE; these expected flight directions are consistent with what we observed. Crossing Lake Erie in its eastern half may happen more frequently if birds fly NE along the south coast of Lake Erie before crossing, given the coast is oriented at an angle of about 60° which is approaching the angle of travel. This type of coast-following behavior on the S coast of Lake Erie was frequently observed near dawn by Archibald et al. (2016) and is also reported in a marine radar study (Horton et al. 2016b). Buler and Dawson (2014) found evidence from U.S. weather radars that many birds stopover in spring on the south coast of Lake Erie directly south of where we found the highest bird density in our study.

We also found some evidence of smaller concentrations along the coast of Lake Huron, as evidenced by the higher densities along the south end of the lake compared to farther inland, mid-way between Lake Huron and Lake Erie (Fig. 3, Table 3D, group 9 compared to group 8). Otherwise, bird densities were much lower along the eastern coast of Lake Huron compared to mid-way between Lake Huron and Lake Ontario (Table 3D, group 10 compared to group 6). These may be birds that shifted to overland flights after crossing part of the southern end of Lake Huron. Such birds could continue ENE to round Georgian Bay or may continue northwards toward the Bruce Peninsula.

Explaining the migration pattern in southern Ontario

The configuration of the lakes surrounding southern Ontario explains the main flyway observed on the eastern side of the study area. The terrestrial shape creates a land bridge oriented NE–SW connecting the large forested breeding ranges of northeastern
Ontario/northwestern Quebec and the wintering range in USA, and Central and South Americas, with the lakes forming potential barriers on either side, with greater expanses of water on the western side of the study area. This is a similar orientation to the land mass in Western Europe, where many birds fly NE–SW across the Iberian Peninsula, avoiding the barriers of the Atlantic Ocean and Mediterranean Sea on either side (Weisshaupt et al. 2018, Nilsson et al. 2019), although southern Ontario forms a smaller land mass and the Great Lakes are smaller barriers.

Previous studies have also shown that flight directions of nocturnal passerine migrants in much of NE North America have a SW component in autumn (Lowery and Newman 1966, Richardson 1972, Horton et al. 2016a, Dokter et al. 2018b) and a NE component in spring (Richardson 1971, Gauthreaux et al. 2003, Farnsworth et al. 2016, Horton et al. 2016b, Dokter et al. 2018b). In general, we would anticipate birds to fly S in autumn and N in spring, along the shortest routes connecting breeding and wintering ranges, but these directions may be shaped by a combination of geographic features and wind direction (Alerstam 2011, Kranstauber et al. 2015, La Sorte et al. 2016, Nilsson et al. 2019). As an example, Kranstauber et al. (2015) used simulations of winds for NE North America to suggest that optimal routes would have a SW component in autumn and a NE component in spring. In our study, as in the above mentioned on flight direction in the NE North America, it appears also that major geographic features might help to explain orientation/navigation decisions, which are recognized in addition to main navigational cues for night migrants, such as the polarized light, the stars and the magnetic field (Martin 1990, Alerstam 1996, La Sorte et al. 2016). In that specific area of North America, several geographical features are oriented in a generally NE–SW direction, including the Appalachian Mountains, the Atlantic Ocean north of Boston, the St. Lawrence River and estuary, and the lower Great Lakes. In Europe, there is also evidence that migration routes are dictated by the configuration of geographical features (Berthold and Hérbig 1992, Nilsson et al. 2019). In addition, stopover habitats might influence the pattern of these night migrants where the amount of hardwood forest cover in the landscape seems decisive (Buler and Moore 2011, Lafleur et al. 2016), which is more important in the east of the study area (Statistics Canada 2013). In this regard, Buler and Dawson (2014) found some evidence that the southeastern coast of Lake Erie was used as a stopover habitat in fall. Large cities with bright light sources might attract birds in active migration (McLaren et al. 2018), which might be the case for Toronto and its suburbs in our study area, but light pollution can be confounded with important migration passage areas, as this pollution is greatest in these areas (Cabrera-Cruz et al. 2018).

We found that birds frequently shifted orientation later in the night, especially in the autumn, generally in a clockwise direction, as observed in other studies in NE North America (Gagnon et al. 2011a, Farnsworth et al. 2016). These shifts are consistent with birds being particularly likely to avoid overwater crossings later in the night (Bruderer and Liechti 1998, Diehl 2003, Gagnon et al. 2011a, Desholm et al. 2014). We found some shifts in spring migration to directions avoiding Georgian Bay many tens of kilometers before the birds would have reached the shore. While it is possible the birds are seeing the barrier at that distance, another possibility is that they are remembering their route from the previous autumn, which they are largely following in reverse. There is evidence that many migratory passerines, including North American species, have long-term memory (Mettke-Hofmann and Gwinner 2003, Mettke-Hofmann 2016) and are able to remember high-quality stopover or wintering sites until the next year (Rappole and Jones 2003) and to collect spatial information while on migration (Healy et al. 1996). As an example, birds aloft can access sensory information from audible cues such as coastal edge (D’Arms and Griffin 1972, Griffin and Hopkins 1974) and visual cues such as topographical landmarks (Martin 1990, Alerstam 1996).

Conclusions and future directions
Overall, we found evidence supporting our hypotheses that the Great Lakes shape the migration of nocturnal passerines in southern Ontario in terms of flight direction and bird density. We found the highest bird densities during active migration in the southeast of southern Ontario (southeast of a line drawn from the southern tip of Georgian Bay to the southern tip of the main basin of Lake Huron), with bird migration frequently concentrating along the edges of lakes.

These concentrations occur in some of the most heavily developed areas of Ontario, including the large urban centers of Toronto, Hamilton, and cities between, creating potential conservation concerns. Artificial light at night from large urban centers can significantly impact both active migrants (Van Doren et al. 2017) and birds seeking stopover locations (McLaren et al. 2018). Birds attracted into the cities face many potential hazards, especially from collisions (Calvert et al. 2013, Los et al. 2014, Lao et al. 2020). Limited availability of good-quality foraging habitat in this region may enhance the value of remaining green spaces. Further studies of birds as they land at dawn or take off at dusk are needed to understand the importance of stopover sites in these areas.

Recent developments in automated extraction and computation of bird migration metrics from WSR (Dokter et al. 2018a) could facilitate further evaluation of the patterns we observed. Automated analyses (Dokter et al. 2018a) have led to increased use of WSR for continental scale analyses of bird migration. Recent studies looked at geographic variation in density of migrants using individual radars as sampling units (Farnsworth et al. 2016), estimated total migratory flux among seasons across North America (Dokter et al. 2018b), and examined large scale patterns of migration in Europe (Weisshaupt et al. 2018, Nilsson et al. 2019). Automated analyses would facilitate processing much larger volumes of data than we were able to analyze with our semi-manual approach. Examining data throughout the night, instead of only two time periods, as well as from additional radars and seasons, would allow quantitative estimation of the numbers of birds crossing the lakes or going around them, and understanding the weather conditions that facilitate lake crossing or encourage lake avoidance. They would also allow improved understanding of take-off and landing sites by determining where birds appear at dusk or disappear at dawn.

However, some further refinements to the algorithms are still needed to examine smaller-scale patterns around each radar. Dokter et al. (2018a) estimated the total density of birds around a radar using an average RCS, ignoring the orientation of the birds. However, the RCS exhibits an angular dependence on...
whether birds are facing the radar or flying perpendicular to the beam (Vaughn 1985, Chilson et al. 2012), which needs to be considered to estimate local variation in density. We accounted for this by only comparing densities between sectors where birds were oriented in a similar direction relative to the radar. An automated analysis could potentially calculate the orientation and migration direction of birds in all sectors (Farnsworth et al. 2014) and then combine that with quantitative data on how RCS of birds changes with the angle to estimate corrected densities in all directions.

Ongoing upgrades to the CWSR network will also facilitate future analyses. The CWSR radars are being upgraded from single polarized C-band radars to dual-polarized S-band radars with up to 240 km Doppler range. Twenty of the 32 CWSRs are scheduled for replacement by 2023 (ECCC 2017). These new CWSRs will be comparable to the current U.S. WSRs, allowing detection of birds to a much greater distance, thus covering a greater portion of the Great Lakes using the radars we studied. Simultaneous analysis of data from radars on both sides of the lakes would allow robust analysis of movement around all of the lakes.

Responses to this article can be read online at: https://www.ace-eco.org/issues/responses.php/2118

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Appendix #1

Study area and radar data

Radar characteristics
Both of these radars were C-band radars characterized by a wave length of 5.32 cm, a beam width of 0.65°, a peak power of 250 kW, and a gain of 47.5 dB (Joe et al. 1998). The radar processor normalized the reflectivity values in relation to range ($R$) to account for the decrease of reflectivity ($Z$) with range at a rate proportional to $1/R^2$ assuming that targets fill the radar beam. The radars collected data over a 10-min period in three different modes: 5-min scans measuring the conventional volume (CONVOL) followed by 5-min scans measuring two different Doppler volumes (DOPVOL1 and DOPVOL2; (Joe and Lapczak 2002). We used data from two of these modes, CONVOL and DOPVOL1. In CONVOL mode, the radar has a pulse length of 2 µs and scans at 24 different angles, starting at 0.3° and increasing by 0.2° for the next four angles, up to 24.7° (Joe and Lapczak 2002). It provides unfiltered total reflectivity data ($Z_t$ in dBZ), including clutter (echoes from structures on the ground) over a 256 km range. In DOPVOL1 mode, the radar has a pulse length of 0.8 µs and provides a measure of reflectivity filtered to remove clutter ($Z_t-Z_c$ in dBZ) and a velocity azimuth display (VAD) for moving targets (in m s$^{-1}$) over a 113 km range with three scanning angles at 0.5°, 1.5° and 3.5°. In both modes, we used only data collected at an elevation angle of 0.5°. We based most of our analyses on the DOPVOL1 data, which provides information on flight direction and excludes clutter, but the CONVOL data are more sensitive for detecting birds, and we used it to provide density information for some areas on nights when migration activity was below average.

Radar analysis
We processed the radar data manually, with one person (FG) reviewing and analysing all images, to minimize the risk of bias affecting fine scale spatial analyses. This method differs of the automated software approaches that have been developed more recently for distinguishing bird echoes from those of weather or clutter for both S-band radars such as those used in the United States as well as C-band radars (Chilson et al. 2018, Dokter et al. 2018a, Lin et al. 2019). However, the later approaches work best for dual-polarization radars (Kilambi et al. 2018), which was only the case for one of our radars, and they are most appropriate for large-scale analyses, as not all echoes are correctly classified. Furthermore, existing automated algorithms do not address issues such as variation in echo strength associated with the angle of detection of the bird (Dokter et al. 2018a) or errors due to anomalous propagation (Kilambi et al. 2018). Thus,
manual review of all images, and careful selection of areas for analysis, allowed us to minimize risks of bias.

We used two proprietary software packages to view the images and extract relevant information: RAPID, developed by the J.S. Marshall Radar Observatory (McGill University, Montreal, QC, Canada) and URP developed by the Meteorological Service of Canada (Environment Canada and Climate Change, Government of Canada). RAPID allows visualizing data at 1 km² resolution cell for any volume, while URP has a cell resolution of 1° x 1 km for CONVOL and 0.5° x 0.5 km for DOPVOL1. RAPID was used to inspect radar imagery for the selection of nights and to estimate flight directions and flight speeds. URP was used to estimate bird densities. Within the URP software, a block of 3° x 3 km, has 9 cells in CONVOL and 36 cells in DOPVOL.

We differentiated precipitation from biological targets through visual inspection of the radar images using the RAPID software. Areas of precipitation were identified based on generally high reflectivity, and relatively uniform movement, often extending long distances from the radars. We considered echoes to be dominated by nocturnal bird migration if they had much weaker reflectivity (we set the threshold to the minimum scale of -22 dBZ), appeared around 30-40 min after sunset, were mainly visible within about 60-80 km of the radar station, and had an average airspeed > 7 m/s at 75-min after sunset (Larkin 1991, Gauthreaux and Belser 1998). The threshold of 7 m/s was selected to reduce the likelihood that echoes were dominated by insects, which generally have much slower airspeeds. Some studies have used a threshold airspeed of 5 m/s to filter birds from insects (ex.: Farnsworth et al. 2016, Horton et al. 2016) or no threshold (Dokter et al. 2018b), but supplemented this with additional analyses to measure variance in airspeeds using a root means standard error filter (see Dokter et al. 2011). We felt that using a higher threshold without the additional filter would be equally effective, especially as our goals related to variation among sites in bird migration rather than estimating the absolute number of migrants. We estimated the air speed of targets by calculating the maximum velocity (VAD) from the DOPVOL1 product shortly after take-off, and using vector arithmetic to calculate the difference from the wind velocity at a similar altitude obtained from atmospheric soundings made at 00h00 UTC at the DTX and BUF weather stations. For WKR, the wind vector from BUF was used, while for WSO the mean wind vector from BUF and DTX stations was used, because WSO was located at mid-distance between these stations. Some study as Nilsson et al. (2019) have used NCEP reanalysis providing higher resolution of spatial and temporal wind profile; other reanalysis such as NARR or ERA5 (30 km grid resolution) could be used too. For each night, two measurements of the target's air speed were computed at different altitudes using wind data.
taken around 610 and 914 m above sea level (asl). If either measurement of the air speed of targets was > 7 m/s, then targets were considered to be dominated by birds and the radar data were included in the analyses.

Estimating bird density
In most cases, we used data from DOPVOL1 to estimate relative densities, as this product excludes ground clutter. However, on some nights when migration intensity was low and could not be detected on DOPVOL1, we used the CONVOL data. On any given night, for a given group of blocks, we only used data of the same type of volume to enhance comparability of analyses within groups.

We filtered the reflectivity data using various approaches to remove unwanted echoes. First, we viewed animations of the radar data over the night to detect and exclude any blocks on that night or time, with evidence of echoes caused by abnormal propagation, precipitation, or clutter. We further eliminated any individual cells within a block having reflectivity > 20 dBZ which is higher than any normal bird migration, and likely indicates echoes from non-bird targets. We then excluded any block with fewer than 5 cells remaining. Next, we applied a recursive median filter to eliminate any cells where the η value exceed 2.5 times the median value among all cells of the same block at a given night and time until the median stabilized. A median filter is a common technique of noise attenuation in imagery (Yin et al. 1996). The threshold value of the median filter was chosen after a graphical exploration of the data relative to the median. A graphical verification of the data after filtration showed that these approaches were efficient at eliminating the vast majority of outlying values. Finally, before running the statistical analysis, the data were plotted to verify and eliminate outliers not removed by the filters (i.e., anomalously large values in comparison to other blocks of the same group) and to exclude any block with fewer than 3 cells remaining. For the reflectivity data, only nights with ≥ 3 groups for a given radar were retained.
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Appendix #2

Statistical analysis

Analysis of flight directions
Circular data analysis were done using the R package circular 0.4-93 (Agostinelli and Lund 2017). To display the central tendency of the raw data for flight directions, the circular median is preferable to the circular mean as it is less affected by outliers (Otieno and Anderson-Cook 2006). However, for statistical comparisons of changes in flight direction over the night for each of the 12 azimuthal points, we calculated the circular mean; the 95% confidence intervals (CI) of these means, each generated with 9999 bootstrap replicates using the parameter of a vonMises distribution. If the 95% CIs excluded 0°, we concluded we had evidence of a change of flight direction during the night (no change [Pewsey et al. 2013]). The tests were conducted for paired-samples only at locations with sufficient data for ≥ 5 nights.

Raw nightly observations of flight directions
The raw nightly observations of flight directions measured at 40 km range are also presented in circular plots separately for each radar and each season, at the four azimuthal points, to show the distribution and variation in flight patterns among nights.

Circular statistics summaries on flight directions
We computed the median and the mean deviation for the median, the skewness and the kurtosis along with their 95% bootstrap CIs using R code found in Pewsey et al. (2013; chapter 5), and compared them using the test of common medians (Fisher’s nonparametric test) and the test of common distributions (large-sample Mardia-Watson-Wheeler test) with the R code in Pewsey et al. (2013; chapter 7).

Comparing bird density between radars
We calculated the mean bird density η at each radar, night and time. We used LMM to model the natural log of the mean bird density for which we had minimally data in n ≥ 10 blocks at each radar, night and time, against the fixed effects of radar and time of night (factorial) with their two-way interaction, and the random effect of night as a random intercept. Nights were weighted by the inverse of the variance in bird density η among blocks within each radar following meta-analysis principles. We fitted the models using the nlme 3.1-139 (Pinheiro et al. 2019), with its function ‘lme’ and a fixed variance structure (‘varFixed’) and the argument ‘lmeControl(sigma = 1)’
The estimated marginal means were computed with the R package `emmeans` 1.3.5.1 (Lenth 2019) with statistical contrasts calculated: 1) between radars within time and 2) between times within radar.

**Comparison of bird density within groups of blocks**

We compared bird density among blocks within each group to test whether densities varied over relatively short distances in relation to factors such as coastlines. We used LMM or GLMM, fitted separately by season and by radar to model bird density $\eta$ against the fixed effects group, block nested within group and time with their two- and three-way interactions, and the random effects of night with time as a random slope. Following Zuur et al. (2010), we initially fitted linear mixed effects models (LMM) to the natural log of bird density $\eta$, but if the model did not fit well, based on analyses of residuals, we then modelled raw bird density $\eta$ with a log link using generalized mixed effects models (GLMM), assuming either Gaussian or Gamma residuals, using a likelihood ratio test to determine which model was the best fit (Bolker et al. 2009, Faraway 2016). We used maps to display graphically the estimated marginal means of bird densities $\eta$ from the valid models, for each season and time within groups of blocks. The LMM and GLMM were fitted using the R package `lme4` 1.1-21 (Bates et al. 2015) and the residuals were extracted using the R package `broom` 0.5.2 (Robinson and Hayes 2019). The estimated marginal means were computed with the R package `rcompanion` 2.2.1 (Mangiafico 2019) and `emmeans` 1.3.5.1 (Lenth 2019) with statistical contrasts calculated: 1) between blocks within time and 2) between times within block.

**Comparison of bird density between paired-groups**

To test whether bird density varied at medium scales (i.e., 50 to 100 km) we compared densities between pairs of groups that were symmetrically opposed at similar angles on each side of a centered flight direction on a particular night and time. The centered flight direction was the azimuth of nearest maximum negative or positive velocity measurement on VAD and was allowed to vary of $\pm$ 15°. For these comparisons, we only used nights and times when both groups had data for at least 3 blocks and when the total paired-sample size was $\geq$ 5 within each time. Either LMM or GLMM were fitted for each season and radar separately, using the same protocol as explained in the sections above. Models included fixed effects of group id and time (if there were sufficient data for both times in a pair), and random effects of night with a random intercept, and time as a random slope, if needed. The estimated marginal means were computed with the R package `emmeans` 1.3.5.1 (Lenth 2019) with statistical contrasts calculated between groups within time.
We performed contrasts at $\alpha = 0.05$ with a Tukey adjustment method, and used R 3.6.0 (R Development Core Team 2019) for all statistical analysis.
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Figure A3.1. Nightly flight directions of migratory birds in southern Ontario, Canada, in autumn 2009 to 2011, during nights of high migration intensity, at 2.5h (t1) and 6h (t2)
after sunset, as measured using the King City (WKR) and the Exeter (WSO) Canadian weather surveillance radars. Each arrow indicates an individual nightly measurement of average flight direction at each of four positions relative to the radar (maximum negative velocity [approximately N of each radar]), zero velocity to the left of the general direction of travel [approximately east of each radar], maximum positive velocity [approximately south of each radar], zero velocity to the right of the general direction of travel [approximately west of each radar]), at 20, 40, 60 and sometimes 80 km from each radar if sufficient birds were detected at that distance and direction. Notice that the position of the arrows has been jittered along the range to avoid overlapping arrows. West of WSO, we present an additional measurement made at 30 km range (thin red arrows) to show flight directions near the shoreline of Lake Huron.
Figure A3.2. Nightly flight directions of migratory birds, in southern Ontario, Canada, in spring 2010 and 2011, during nights of high migration intensity, at 2.5h (t1) and 6h (t2) after sunset, as measured using the King City (WKR) and the Exeter (WSO) Canadian weather surveillance radars. Each arrow indicates an individual nightly measurement of average flight direction at each of four positions relative to the radar (maximum negative velocity [approximately south of each radar]), zero velocity to the left of the general direction of travel [approximately west of each radar], maximum positive velocity [approximately north of each radar], zero velocity to the right of the general direction of travel [approximately east of each radar]), at 20, 40, 60 and sometimes 80 km from each radar if sufficient birds were detected at that distance and direction. Notice that the position of the arrows has been jittered along the range to avoid overlapping arrows. West of WSO, we present an additional measurement made at 30 km range (thin red arrows) to show flight directions near the shoreline of Lake Huron.