Research Paper

Migrants employ mixed strategies to route across the Great Lakes basin

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ABSTRACT. Millions of migrants encounter the Great Lakes during spring and autumn migratory movements. How migrants behave when encountering these lakes is relatively unknown at the local and basin scales. Using seven years of radar data from 33 sites along the Great Lakes coastline, we investigated three hypotheses on migrant behavior during crepuscular and nocturnal movements. First, we hypothesized migrants' direction is driven by local geography and its relation to the destination of migration. Second, we hypothesized migrants would move toward shore at dawn. Finally, we hypothesized that the Great Lakes would have different directional movements at lakes on the outside of the basin versus the interior. We found partial support for our first hypothesis, as well as evidence of decision making when migrants first encounter the Great Lakes. We found partial support for our second hypothesis. We found that migrants moved toward land at elevated levels at dawn compared to night during fall migration, but no effect was found during spring. We found support for our final hypothesis during spring migration, but not during fall. This pattern may be because of a combination of geographical, biological, and data bias, and will require additional work to disentangle. Taken together, we found that migrants perceive and react to the Great Lakes, and attempt to decrease risk, perceived or real, as they make their way to their migratory destination. Better understanding of directional movement has conservation implications, including mitigating anthropogenic obstacle collision risk and prioritizing stopover habitat restoration.

Les oiseaux migrateurs utilisent des stratégies mixtes pour traverser le bassin des Grands Lacs

RÉSUMÉ. Des millions d'oiseaux croisent les Grands Lacs au cours des déplacements migratoires de printemps et d'automne. Le comportement des migrateurs lorsqu'ils rencontrent ces lacs est relativement inconnu à l'échelle locale et celle du bassin. En utilisant sept années de données radar provenant de 33 sites le long des côtes des Grands Lacs, nous avons examiné trois hypothèses sur le comportement des migrateurs pendant les déplacements crépusculaires et nocturnes. Notre première hypothèse veut que la direction des migrateurs soit déterminée par la géographie locale et sa relation avec la destination de la migration. Notre deuxième hypothèse stipule que les migrateurs se déplaceraient vers la côte à l'aube. Enfin, notre dernière hypothèse suppose que les déplacements directionnels au-dessus des Grands Lacs seraient différents selon que les lacs se trouvent à l'extérieur ou à l'intérieur du bassin. Notre première hypothèse a obtenu un soutien partiel, et nous avons trouvé des indices de prise de décision lorsque les migrateurs rencontrent les Grands Lacs pour la première fois. Notre deuxième hypothèse a aussi reçu un soutien partiel : nous avons constaté que les migrateurs se déplaçaient vers la terre ferme à des taux élevés à l'aube par rapport à la nuit pendant la migration d'automne, mais aucun effet n'a été constaté au printemps. Notre dernière hypothèse a été confirmée au cours de la migration printanière, mais pas lors de celle d'automne. Ce schéma peut être dû à une combinaison de biais géographiques, biologiques et de données, et nécessitera des travaux supplémentaires pour qu'on comprenne mieux. Dans l'ensemble, nous avons constaté que les migrateurs perçoivent les Grands Lacs et y réagissent, et qu'ils tentent de réduire les risques, perçus ou réels, lorsqu'ils se dirigent vers leur destination migratoire. Une meilleure compréhension du déplacement directionnel a des implications en matière de conservation, y compris l'atténuation du risque de collision avec des obstacles anthropiques et la priorisation de la restauration des habitats utilisés pendant les haltes migratoires.

INTRODUCTION

Long-distance migration is a complex behavior; migrants face risks and obstacles and have limited information about environmental conditions and geography when choosing strategies to minimize risk. Although migration occurs in a number of taxa, aerial nocturnal migrations of birds constitute some of the most challenging and impressive migratory patterns known (Thorup et al. 2007). Of particular interest is how aerial migrants contend with obstacles to migration during their journeys, especially open water. Most aerial migrants are unable to safely land on water and are unable to swim or thermoregulate effectively in water environments, making open water crossing, and the threat of being forced to land there because of exhaustion or weather, especially dangerous (McClintock et al. 1978, Newton 2007). Because terrestrial migrants require land for stopover, crossing large bodies of water with limited resources constitutes a risk, whether large or small, for migrants.

Migratory birds face increasing threats globally (Wilcove and Wikelski 2008, Gilroy et al. 2016), with many species in steep decline across North America (Rosenberg et al. 2019). Migrants may face potential mass mortality during the migration period

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(Sillett and Holmes 2002, Newton 2006, Newton 2007, Diehl et al. 2014) and losses around ecological barriers such as water crossings may be a contributing factor to declines. To address declines of migratory species, we need a better understanding of the spatial and temporal aspects of migration, especially at obstacles where there is potentially increased risk. By better understanding how migrants use shorelines and where and when water crossings occur, we can better implement conservation and restoration activities to reduce the risk associated with water-crossing behaviors (Smolinsky et al. 2013, Ward et al. 2018). Of particular importance is understanding flight behaviors, including how migrants use airspace over land and water and whether they cross open water or follow the shoreline. Understanding how flight behaviors are affected by differences in season, time period, and region will allow for better management and mitigation programs, such as lighting policies for buildings or municipalities and scheduled curtailment for wind turbines.

Migrating aerial vertebrates in the eastern Americas are likely to encounter various major water crossings en route, including the Gulf of Mexico, the Caribbean Sea, and the Laurentian Great Lakes. Substantial progress has been made in understanding the behaviors of migrants crossing the Gulf of Mexico and Caribbean (Gauthreaux 1971, Stutchbury et al. 2009, Deppe et al. 2015), but less work has been done on understanding migrant behaviors along the Great Lakes (but see Perkins 1964, Diehl et al. 2003). The Great Lakes are a potential ecological obstacle to migration for many inland North American migrants east of the Mississippi River during autumn and spring (Diehl et al. 2003). Although lake crossings are substantially shorter in duration than other crossings, migrant mass mortality has been documented (Perkins 1964, Diehl et al. 2014). Furthermore, whereas each lake individually may be relatively small, the effect of lakes in aggregate may change migrant behavior that is responding to the Great Lakes basin at a broader scale. Finally, the land adjacent to the Great Lakes region is home to ~33 million people, with human development at the shoreline often in conflict with habitat used by migrants (Wolter et al. 2006). Increasing our understanding of migrant behavior at Great Lakes coastal areas would help highlight areas that are particularly important for the successful completion of migration, such as lake-crossing points or areas of high migrant concentration.

The context under which migrants encounter the Great Lakes may provoke different responses. Differences in local geography, such as the orientation of local lakeshores in relation to the migrants' destination, may be important cues to decision making in relation to crossing the lakes. Previous work has shown that migrants react to a water obstacle either by continuing to cross or by changing their direction to avoid a potentially risky water crossing (Diehl et al. 2003). In addition, migrants may change their strategies depending on the diel cycle. Migrants have been documented to change their flight direction to orient toward shores at dawn (Diehl et al. 2003, Archibald et al. 2017, Heist et al. 2018), likely to find refuges to rest and feed during the day. However, it is unclear if these findings are consistent throughout the Great Lakes region. In addition, it is unclear how migrants may use the shoreline during dusk: they may ignore the shoreline, take advantage of the less cluttered horizon for celestial navigation, or take advantage of offshore breezes when crossing

the lakes (Nisbet et al. 1968, Emlen 1975, Moore 1987). Finally, how or if migrants perceive the lakes as a barrier to migration is unclear: migrants may treat each lake as a distinct entity to cross or they may use routes that are consistent with crossing or navigating the basin as a whole, concentrating migrants at the safest and least energetically costly navigation and crossing points in the basin. In particular, migrants near the eastern and western edges of the basin may show different behaviors, especially if migrants concentrate along shorelines as they circumvent the water or use optimal crossing points.

For this study, we investigated behaviors of migrant birds in response to encountering the Great Lakes. To capture the potential advantages or challenges that shores present to migrants, we classified shores into three major categories: arriving, departing, and parallel shores. Arriving shores were oriented perpendicularly to the main direction of migration (north in spring, south in autumn) and with the radar situated so that migrants must cross open water before being detected if they followed the main direction of migration. Departing shores had the same east-to-west orientation as arriving shores, but with the radar situated so that migrants would venture from land to open water at the site if they followed the main direction of migration. Parallel shores were oriented approximately parallel to the main direction of migration, and migrants would move along the shoreline if they followed the main direction of migration. These categories imply an opportunity for migrants to make a directional decision on the basis of geographical context, such as when encountering open water after traveling over land or vice versa. Although any migrant over a lake can be considered to be moving toward some land, by focusing on locations adjacent to shorelines, we assumed migrants would perceive the direction of movement to the nearest land to be "landward" movement and the opposite direction to be "waterward" or away from land.

We tested three hypotheses regarding migrant orientation, depending on the shoreline, time period, and lakes. Our first hypothesis was that migrants choose their direction on the basis of the orientation of the local shoreline rather than solely on orienting toward the destination. The null hypothesis for migrants encountering the Great Lakes was that they would travel in the main direction of migration (north in spring and south in autumn), with an alternate hypothesis that the direction of travel would deviate toward the east or west depending on shoreline type. Grouping sites into shoreline categories allowed us to assess whether migrants' strategies differed on the basis of the local geographical context. We expected that these strategies would be similar across seasons and investigated the hypothesis at dusk and at night to see if migrants employed different strategies at different times.

Our second hypothesis was that migrants at dawn in all shoreline categories would move toward the nearest land and avoid crossing water in order to seek shelter and move off the water rather than continuing toward their final destination. The null hypothesis was that migrants would move in the main direction of migration at dawn and the alternate hypothesis was that they would move toward land. We expected shifts to be most notable for shorelines where migrant directional movement and land-seeking movement were in opposition. Specifically, we expected a reversal in direction at departing shores, reflecting migrants over the lake reversing direction and heading back to the nearest shore.

Our third hypothesis was that migrants would react to the Great Lakes basin as a whole. To test this hypothesis, we divided sites into three categories (east, west, and central) and compared migrant movements at night. Our null hypothesis was that there would be no effect when easterly and westerly movements were compared. For the spring, our alternate hypothesis was that the wedge shape of the Great Lakes basin would cause migrants to bifurcate in selecting their routes, resulting in more easterly movements on the eastern side of the basin and more westerly movements for the western side. For the autumn, our alternate hypothesis was that any bifurcation would occur north of our study sites and we would observe migrants moving from the east and west to fill in the central area, producing more westerly movements on the eastern side of the basin and more easterly movements on the western side in autumn.

METHODS

From 2011 to 2018, we collected radar data at 33 coastal sites across the U.S. coastline of the Great Lakes (18 spring, 14 autumn; Appendix 1) using two SS200DE MERLIN Avian Radar Systems (DeTect Inc., Panama City, FL, USA), using methods outlined by Rathbun et al. (2016). Solid state marine radar antennas (LPA-3 Sharpeye; Kelvin Hughes, London, UK) employed by our systems had 170 W peak power, S-band (10 cm) wavelength, 2.92–3.08 GHz frequency range, and were configured to operate with both short and medium pulse (0.1 and 5 microseconds, respectively) simultaneously in order to optimize the return at different distances from the antenna. In operation, we used both horizontal and vertically oriented radar antennas; for the purposes of this study, we focus on the horizontal component only. The radars emanated a fan-shaped beam that had an approximate 1° horizontal and 25° vertical span when operated in the horizontal plane. The radars spun perpendicular to each other at a rate of 20 revolutions per minute and were synchronized so as not to emit over one another. The horizontal scanning radar (HSR) was affixed to a telescoping base that was raised to 7 m above ground for operation. This radar rotated in the x-y plane with a 7° tilt to reduce the amount of ground clutter included within its view, resulting in a scan from roughly 0–20° above the horizon. Although the radar had the capability of scanning to longer distances (to 11.1 km), the beam power and subsequent ability to detect small targets such as passerine birds declines with distance. We therefore selected a shorter, 3.7 km range setting for data collection to provide resolution and tracking on smaller targets such as passerines and bats, although target detection may still have been reduced for smaller birds at the extremes of this range. In this setting, the radar emits the same power output as the 11 km setting, but the software only tracks and retains targets within 3.7 km. The horizontal radar employed Doppler shifts to help filter out stationary targets. Doppler shifts occur only on objects moving in relation to the radar unit and the radar categorizes non-shifted radar reflections as stationary objects, not migrants. Targets that are moving precisely perpendicular to the radar may be lost because of a lack of Doppler shift, but given the tracking algorithm (discussed below), we anticipate very few targets being left untracked because of being perpendicular to the radar beam.

The MERLIN software tracks targets using linear and curvilinear predictive models to connect successive radar returns into tracks.

This algorithm uses measurements of location, direction, acceleration, and speed to constrain the predicted flight path of migrants to biologically feasible candidate returns and filters these returns to determine the highest likelihood extension of the track. Tracks with multiple candidate returns are predicted simultaneously, and proposed tracks are omitted or supported on the basis of the fit of the proposed model to subsequent radar returns; these multiple predictions also allow for tracking flocks when they split or merge. Initiation of tracks begins with any radar returns not integrated with any current tracks. Newly initiated tracks must be detected over four successive scans to be recorded as a track; tracks of three or fewer scans are not saved. Radar contact can be lost because of interference or changes in the orientation of migrant orientation to the radar beam. Because of this, the tracking algorithm allows tracks to continue without a radar return, and continues to predict a target location for a set period of scans in anticipation of reacquiring the target on the basis of last location, direction, and acceleration. We allowed tracking to continue for three subsequent scans after target loss.

We minimized false tracks from precipitation events, static clutter, and anthropogenic and invertebrate aerial clutter in several ways. First, we employed S-band radar (approximately 10 cm wavelength) because this wavelength is less sensitive to insect and weather contamination than X-band radar (approximately 3 cm wavelength; Bruderer 1997) at a cost to fine resolution. Combined with clutter suppression, this eliminates almost all insect clutter. We therefore did not employ standard (e.g., airspeed threshold) insect clutter removal methods. S-band radar is also less sensitive to signal attenuation from ground clutter such as vegetation and structures (DeTect Inc., *unpublished data*, 2009). Static clutter (e.g., vegetation, structures) was also mitigated by using a composite of 60 static scans taken during clear air to identify and omit areas of persistent low detection because of clutter. Fixed-winged aircraft move too quickly through the area under radar study for the algorithm to produce tracks. Rotor-winged aircraft moving in relatively straight lines (e.g., from one location to another) are also not tracked, similar to fixed winged aircraft. However, the algorithm does track rotor-winged aircraft if they turn in slow orbits. We only observed this at one site when helicopters were circling a sporting event; the signature of a nearly perfect circular track was diagnosed and omitted from the dataset during reviews for precipitation (discussed below).

We employed an automated filter to remove sectors of the sample volume that were dominated by precipitation, insects, and other clutter. During some time periods, however, the automated filter did not remove all precipitation from the recorded outputs. We relied on visual inspection of track patterns to discern contamination events. DeTect software outputs included a two-dimensional digital display of target tracks over a specified period of time (Trackplots) for horizontal radars. We reviewed Trackplots in 15-min increments to evaluate the data for potential contamination by non-targets. Rain and precipitation events form diagnostic patterns of unconnected "points" on the horizontal radar, driven by the tracking algorithm connecting closely spaced raindrops (DeTect Inc., *personal communication*, 2011) instead of longer tracks diagnostic of biological targets. We removed data from time periods that were dominated by

Fig. 1. Sampling scheme for directional analysis. Radar site is the black circle, while shading indicates land, and the grey line indicates the coast. Radar data is divided directionally in order to capture movements in multiple broad orientations simultaneously. Movement in the 'Water' direction indicates migrants moving towards the lake or away from land. Movement in the 'land' direction indicates movement toward inland locations or away from water. Movement in the 'migratory coastal' and 'counter-migratory coastal' directions indicate concurrence and non-concurrence (respectively) with the dominant direction of migration (north in summer, south in winter). a) depicts the sampling scheme at a shoreline oriented roughly parallel to the main movement of migration, while b) and c) depict the same sampling at shorelines where migrants would be departing and arriving, respectively.
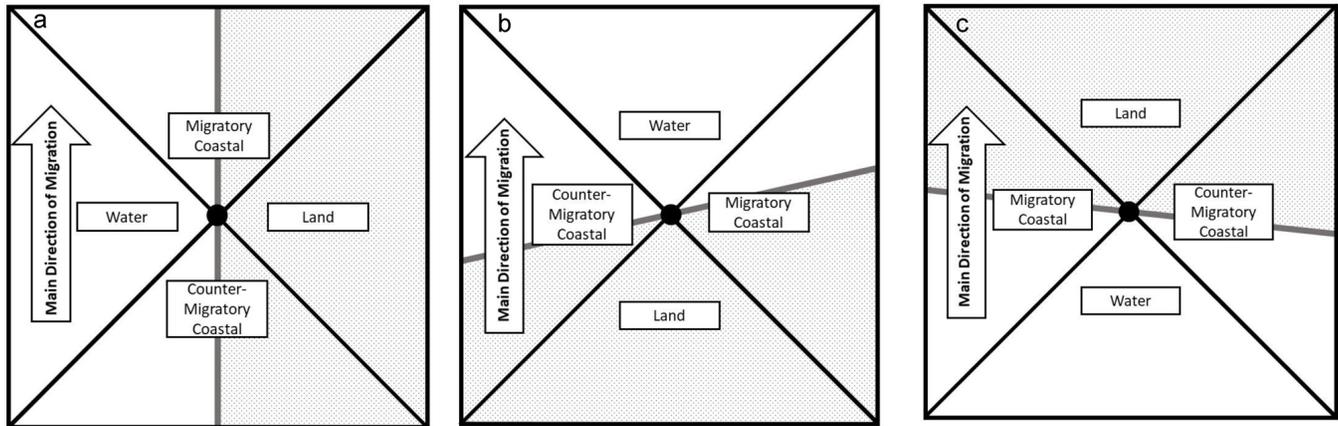
precipitation clutter from further analysis. There may still be unknown contamination that mimicked patterns of desired targets we were not able to remove from the database and, to the extent that this occurred, contributed to error associated with indices.

Each target track was assigned one of the eight cardinal and intercardinal directions by the MERLIN software. We collected data continuously for the season (autumn: ~1 August–10 November; spring: ~1 April–10 June) and surveyed during at least one spring and one autumn migratory season for each of the five Great Lakes.

We confined our analysis to night and crepuscular movement because daytime migration may include uncertainty from non-migratory species or non-migratory behaviors (e.g., foraging during stopover). We summarized tracks in three biological periods: dawn, defined as 30 minutes before and after sunrise; dusk, defined as 30 minutes before and after sunset; and night, defined as 30 minutes after sunset to 30 minutes before sunrise.

Directional analysis

We analyzed directional movement patterns to capture the behavior of migrants across the Great Lakes basin. We focused on detecting directional movement in relation to water and land at shoreline locations for hypotheses one and two, and movement in each of the eight cardinal and intercardinal directions for hypothesis three.

Because thousands to millions of target tracks were included in these samples (range of tracks, night: 215,967–29,041,490; dusk: 4,871–787,728; dawn: 13,427–1,935,953), hypothesis testing for statistical significance would produce significant results even from biologically irrelevant differences in samples. We instead assessed the effect size of differences in migrant movements, using Cohen's h as our metric (Cohen 1988). Cohen's h is a metric for the difference between the arcsin transformation of the probabilities of two proportions, p:

$$\phi = \arcsin\left(\sqrt{p}\right) \qquad (1)$$

and

$$h = \phi_1 - \phi_2 \qquad (2)$$

The result is an effect size $0 < |h| < 1$, with greater effect as $|h|$ approaches 1. In addition, Cohen's h provides polarity of signal, allowing us to determine whether movements were positive (greater than expected) or negative (less than expected) in a particular direction.

When testing our first two hypotheses, we divided migrant directional movements into four 90° categories defined by the local shoreline angle and ultimate migratory goal: land, water, migratory coastal, or counter-migratory coastal directions (Fig. 1). The water direction category was defined as perpendicular to the local shoreline in the direction of the lake and the land direction category was defined as perpendicular to the local shoreline in the direction of land (opposite of the water direction; Fig. 1). For the directional categories perpendicular to the land and water, we assumed that migrants following the coast would prefer movement at least partially toward the main direction of migration. Thus, we assigned the migratory coastal direction a priori that would allow more northerly travel in spring and more southerly travel in autumn and assigned the counter-migratory coastal direction category in the opposite direction. One site on Lake Ontario was located at the edge of a shallow bay, which produced migratory coastal and counter-migratory coastal designations at odds with the larger coastal geography of the lake. We reversed the migratory coastal and counter-migratory coastal directions at that site to align with the broader geography.

To determine site-specific counts of migrants in each of the four directional categories, we assigned each target track direction (one

of eight cardinal and intercardinal directions) to one of the four directional categories on the basis of the angle of the shoreline at the site. When the angle of the shoreline split a target track direction, we divided the count in that direction proportionally between categories. For example, if a shoreline ran exactly north-south, with the lake to the west, the land category would include all targets moving east and half of the targets each in the northeast and southeast directions (Fig. 1). This approach simplified our examination of decision making for migrants and provided a uniform way to consider orientation of migrants with regard to the coast. We calculated the proportion of migrants in each directional category for each site, and averaged these proportions for each shoreline category (Appendix 2). We conducted tests for spring and autumn separately for all hypotheses.

Hypotheses one and two state that local coastal orientation would affect direction of travel during migration. To investigate these hypotheses, we classified sites into three mutually exclusive categories relative to the lake and the main direction of migration (north in spring, south in autumn): arriving, departing, and parallel. Sites with arriving shores were defined by having the lake situated opposite the main direction of migration (lake was to the south during spring and to the north during autumn). Sites with departing shores were defined by having the lake and main direction of migration in the same direction (lake was to the north during spring and to the south in the autumn). Sites with parallel shores were defined as having shorelines roughly (within 30°) parallel to the main direction of migration.

For hypothesis one, we performed three pairwise comparisons of the proportion of migrants moving in the main direction of migration (landward movement at arriving shorelines, waterward movement at departing shorelines, and migratory coastal movement at parallel shorelines). We conducted comparisons separately for night and dusk periods. We expected that if migrants ignored the coastline, these proportions would be similar (i.e., $|h| < 0.2$); alternately, if shoreline affected migrant direction, we would see differences ($|h| > 0.2$) among shoreline categories. When $|h| > 0.2$, we investigated movements orthogonal to the main direction of migration, assuming that movement directly away from the main direction of migration would be uncommon and unaffected by shorelines. We performed pairwise post hoc comparisons between shoreline categories for directions orthogonal to the main direction of migration (coastal directions for arriving/departing shores and land/water for parallel shores).

We tested hypothesis two by comparing the proportion of migrants moving landward between night and dawn for parallel and departing shorelines, with a null hypothesis that there would be no effect of time period on the proportion of landward movement and an alternate hypothesis that landward movement would be greater at dawn. We tested hypothesis two only at departing and parallel shores because the direction of movement would be toward land under both the null and alternate hypotheses for arriving shorelines.

To test hypothesis three, we classified sites into three regional groups (eastern, western, and central) according to their location within the Great Lakes basin. The eastern group included all sites on Lake Erie and Lake Ontario, the central group included all sites on the lower peninsula of Michigan (western shores of Lake

Huron, eastern shores of Lake Michigan) and the southeastern side of Lake Superior, and the western group included sites on western shore of Lake Michigan and western Lake Superior (Appendix 2). Separately for spring and autumn, we conducted pairwise comparisons of the proportion of easterly movement (east and northeast) and westerly movement (west and northwest) at night between the eastern, central, and western groups, using Cohen's *h*. For hypothesis three, the null hypothesis was that the proportion of easterly and westerly movements would be similar among groups. The alternate hypothesis for spring was that sites in the eastern group would show more easterly movement than would the western or central groups, and sites in the western group would show more westerly movement than in the eastern or central groups. The alternate hypothesis for autumn was that sites in the eastern group would show more westerly movement than would the western or central groups, and sites in the western group would show more easterly movement than in the eastern or central groups.

RESULTS
We collected radar data at 33 coastal sites across the U.S. portion of the Great Lakes, from 2011 to 2018, with a total of 11 arriving (three spring, eight autumn), 10 departing (eight spring, two autumn), and 12 parallel (seven spring, five autumn) shores (Appendix 2).

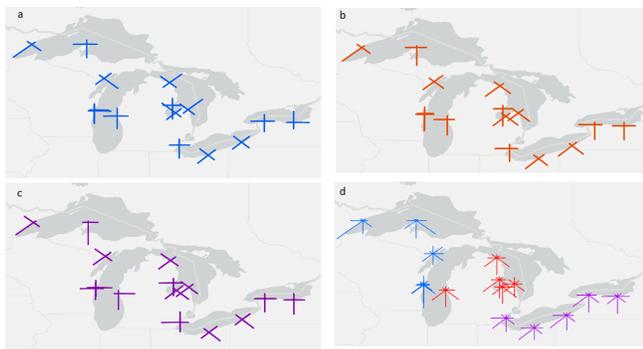### Hypothesis one: shoreline orientation affects migrant direction during dusk and night
During the night time period, arriving and parallel shorelines had a greater proportion of migrant movement in the main direction of migration compared to departing shorelines, supporting our alternate hypothesis at departing shorelines (Table 1, Figs. 2c and 3c). The difference in proportions due to shoreline occurred in both seasons but the effect was greater in autumn than in spring (Table 1). When comparing coastal movements between arriving and departing shorelines post hoc in autumn, we found a greater proportion of migratory coastal movement at departing shorelines but no difference in counter-migratory coastal movement (Table 1), consistent with migrants at departing shores moving along the shoreline in the most efficient route to reach their presumed migratory goal. When comparing coastal migratory movements at departing shorelines with land and water movements at parallel shorelines post hoc in autumn, we found a greater proportion of migratory coastal movement at departing shorelines compared to either land or water movement at parallel shorelines. Differences were much weaker between counter-migratory movement at departing shorelines and either land or water movement at parallel shorelines.

During the dusk time period, we found a greater proportion of movements in the main direction of migration at arriving shorelines than at parallel or departing shorelines (Table 2, Figs. 2b and 3b), providing some support for our alternate hypothesis at arriving shorelines. This effect was not as strong as the effects observed at night (Table 1). A post hoc test comparing the migratory coastal direction at arriving shorelines with the landward direction at parallel shorelines found a greater proportion of migrants moving along the migratory coastal direction of arriving shores compared to the water direction at parallel shores. When comparing post hoc the migratory coastal

Table 1. Cohen's h shoreline category comparisons during night time period, autumn and spring. Positive values indicate the proportion of migrants moving in the main direction of migration is greater in the former shore category, while negative values denote the proportion of migrations moving in the main direction of migration is greater in the latter shore category. We conducted post-hoc tests if |h|>0.2 to determine which direction(s) migrants may be moving other than the main direction of migration. Positive and negative values follow the same conventions as the main direction of migration comparisons. Values of |h| > 0.2 are bolded. Raw proportions for sites and average proportions for shorelines are available in Appendix 1.

Coastal pair in main direction of migration	Autumn	Spring	Post-hoc test	Autumn	Post-hoc test	Autumn	Post-hoc test	Autumn	Post-hoc test	Autumn
Departing shore vs. arriving shore	**-0.320**	-0.192	Migratory coastal departing vs. arriving	**0.236**	Counter-migratory coastal Departing vs. Arriving	-0.028				
Departing shore vs. parallel shore	**-0.380**	-0.169	Departing migratory coastal vs. parallel water	**0.436**	Departing migratory coastal vs. parallel land	**0.556**	Departing counter-migratory coastal vs. parallel water	0.065	Departing counter-migratory coastal vs. parallel land	0.183
Arriving shore vs. parallel shore	-0.060	-0.023								

Fig. 2. Indication of directional movement at all sites during the autumn migration season. Directional movement for each site is broken into 4-direction for figures (a-c). These four directions are indexed on the shoreline, with directions towards water, land, and the coastal migratory and coastal counter-migratory directions. See text and figure 1 for more detail. Figure (d) depicts the 8 cardinal and inter-cardinal directions, with north upwards. Length of each bar is proportional to the number of migrants moving in that direction across the season. Panels a-c depict 4-direction movement for a) dusk, b) night, and c) dawn time periods. Panel d shows the three regions across the region (blue: west region; red: middle region; purple: east region) during night migration.
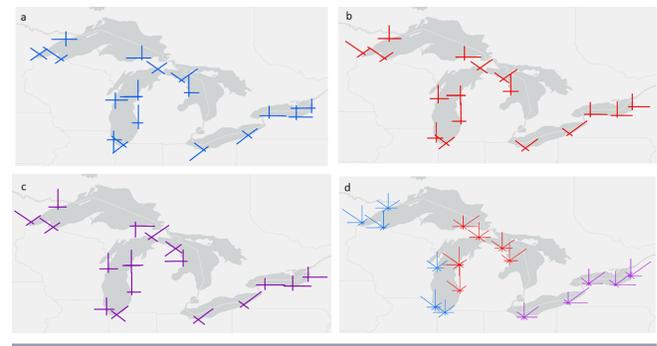

Fig. 3. Indication of directional movement at all sites during the spring migration season. Directional movement for each site is broken into 4-direction for figures (a-c). These four directions are indexed on the shoreline, with directions towards water, land, and the coastal migratory and coastal counter-migratory directions; these directions are chosen as it best describes the categories migrants may decide to use when encountering a lakeshore. See text and figure 1 for more detail. Figure (d) depicts the 8 cardinal and inter-cardinal directions, with north upwards. Length of each bar is proportional to the number of migrants moving in that direction across the season. Panels a-c depict 4-direction movement for a) dusk, b) night, and c) dawn time periods. Panel d shows the three regions across the region (blue: west region; red: middle region; purple: east region) during night migration.

direction at arriving shorelines with the waterward movements at parallel shorelines, we found very weak differences.

Hypothesis two: landward movement will increase at dawn compared to night

We found an increase in landward movement at dawn compared to night at parallel and departing shorelines during spring, supporting our alternate hypothesis. For autumn, we found an increase in landward movement only at departing shorelines, partially supporting the alternate hypothesis (Table 3, Figs. 2a and 3a). Parallel shorelines showed a smaller but opposite trend

during autumn, with a greater proportion of movements away from land (Table 3).

Hypothesis three: migrant direction will be affected by season and location within the Great Lakes basin

During autumn, we found little difference in the proportions of easterly and westerly movements between any regional groups, with the greatest difference being an increase in westerly

Table 2. Cohen's h shoreline category comparisons during dusk. Positive values indicate a greater proportion of movement orthogonal to the main direction of migration for the former of the two shorelines listed, negative values indicate the proportion was greater for the latter shoreline category. Values of |h| > 0.2 are bolded. We conducted post-hoc tests if |h|>0.2 and compared directional movement orthogonal to the main direction of migration for the shoreline categories to determine which direction(s) migrants moved other than the main direction of migration.

Coastal pair in main direction of migration (dusk)	Autumn	Spring	Post-hoc test	Spring	Post-hoc test	Spring
Departing vs. arriving	0.191	0.157	–	–	–	–
Departing vs. parallel	0.004	-0.143	–	–	–	–
Arriving vs. parallel	-0.187	**-0.300**	Parallel land vs. arriving migratory coastal	**-0.394**	Parallel water vs. arriving migratory coastal	0.044

Table 3. Cohen's h shoreline category comparisons for landward movements between the dawn and night time periods, autumn and spring. Positive values indicate the proportion of movement toward land was greater during dawn and negative values indicates the proportion was greater during night. Values of |h| > 0.2 are bolded. Raw proportions for each site and average proportions for each time period are available in Appendix 1.

Coastline	Dawn vs. night, autumn	Dawn vs. night, spring
Departing	**0.358**	**0.360**
Parallel	-0.168	**0.221**

movement for the eastern group (Table 4, Figs. 2d and 3d). These findings support the null hypothesis for autumn overall, with weak support for the alternate hypothesis for the eastern group only. In contrast, we found a greater proportion of easterly movements in the eastern group and greater proportion of westerly movements in the western group in spring (Table 4). These findings support our alternate hypothesis for the spring.

DISCUSSION

Shoreline features and temporal factors (both diurnal and seasonal) influenced migrant bird behavior in the Great Lakes region. At night, migrants moved predominately in the expected direction of migration (north in spring, south in autumn): toward water at departing shores, toward land at arriving shores, and along shore toward their migratory goal at parallel shores. We also found shore-following behaviors as migrants moved in the migratory coastal direction along departing shores, suggesting a mix of behavioral responses as migrants encountered the lakes. At dawn, migrants showed a strong tendency to move to land (at both shoreline types in spring and at departing shorelines only in autumn), consistent with migrants being unwilling to cross the lakes during daylight. At a broad scale, migrant movement was dominantly north in spring and south in autumn, but migrants also shifted their movements at the eastern and western edges of the Great Lakes basin in spring, moving more easterly on the eastern edge and more westerly on the western edge. Our expectation of an opposite pattern in autumn was not as well supported, with only slightly greater westerly movements observed for the eastern group.

Nocturnal movement is largely in the main direction of migration, but departing shores show deviations

Nocturnal directional movement (Table 1, Figs. 2c and 3c) was mostly consistent with nocturnal migrants moving in the direction of their ultimate migratory goal. However, different coastal orientations provide differing opportunities to determine how migrants make decisions on navigating across the basin. Arriving shores may be less informative, because detected migrants have already made the decision to cross the lake. In contrast, departing shores are likely to be a decision point for migrants to cross or go around a lake. At departing shores, we found decreased nocturnal movement in the main direction of migration compared to both parallel and arriving shores, with a stronger effect in the autumn than in spring. Our post hoc analyses showed that the reduction of movement in the main direction of migration resulted in an increase in migratory coastal movements. Overall, this suggests many migrants chose to cross the lakes following the main direction of migration, although a substantial proportion opted against crossing, instead following the shoreline in a way that allowed some progress to their migratory goal.

It is not immediately clear what factors affect migrant decisions in choosing to cross a lake or follow the shoreline in the direction most advantageous to migration. Nocturnal data were pooled across many sites, many nights, and over many hours during the night, so it is unclear if a mix of strategies are being employed by individual birds each night, whether strategies vary among sites or among nights, or if migrants shift strategies as they encounter the lake closer to dawn. Several of these effects could be teased apart from the data collected at specific sites, especially across- and within-night shifts in directional travel. Regardless, this combination of crossing and shore following shows that migrants at night perceive the lakes as they encounter them and are making decisions on whether to cross the lake or follow the shoreline.

Migrants may make individual- or species-level decisions on whether to cross or navigate around the Great Lakes. Many passerine migrants have substantial variation in their migration routes, even when breeding and wintering grounds are highly concentrated (Rappole and Ramos, 1994; Cohen et al. 2018). Drivers in route variation could be extrinsic, species-level, or individual-level factors. Extrinsic factors include weather: headwinds and tailwinds could inhibit or promote crossing, as well as effects from inclement weather (Diehl et al. 2014, Deppe

Table 4. Table 4: Comparisons of directional movement of migrants among regions of the Great Lakes by compass direction. Positive values of Cohen's h indicate the proportion of directional movement was greater in the former of the two regions, negative values indicate the latter region had a greater proportion. Values of |h| > 0.2 are bolded.

Basin comparisons	N	NE	E	SE	S	SW	W	NW
Autumn								
East vs. west	-0.144	-0.009	0.047	-0.117	-0.051	0.031	0.195	0.039
East vs. central	-0.082	0.036	0.008	-0.151	-0.048	0.073	0.185	-0.034
Central vs. west	-0.062	-0.046	0.039	0.035	-0.002	-0.041	0.009	0.074
Spring								
East vs. west	-0.061	**0.408**	**0.357**	0.014	-0.078	-0.154	**-0.266**	**-0.346**
East vs. central	-0.052	**0.320**	**0.277**	-0.042	**-0.241**	-0.113	-0.198	-0.170
Central vs. west	-0.009	0.088	0.080	0.055	0.163	-0.041	-0.068	-0.176

et al 2015, Streby et al. 2015, Dossman et al. 2016, but see Bolus et al. 2017). Data collected from this study could be used to address these extrinsic factors on a nightly or weekly scale. Intrinsic factors, such as an individual migrant's condition (including fat storage, age, population, and sex), may also play roles in whether to cross (Francis and Cooke 1986, Kissner et al. 2003, Deutschlander and Muheim 2009, Delmore et al. 2012, Deppe et al. 2015). Examples of species-level factors include species' flight capabilities (raptors: Agostini et al. 2015; passerines: Buler et al. 2017) as well as diet, which affects the likelihood of acquiring food on the other side of the lake (e.g., granivores versus insectivores). Additionally, wing and body morphology appear to be changing as a response to climate change (Weeks et al. 2020) and recoveries of aerial predator populations (Lank et al. 2017, but see Anderson et al. 2019 for alternate hypotheses) could change the ability and propensity of some species to cross or detour around the Great Lakes. Teasing apart which factors influenced our radar observations would require species- and/or individual-specific data. Combining radar observations with telemetry data (i.e., migrants of known species, age, and sex) could be a way forward.

Migrants move toward migration goal at dusk, but turn toward shore at dawn

Dusk movements were largely consistent with migratory movement (Table 2, Figs. 2b and 3b). Among the three shoreline categories, there was generally no difference in the main direction of migration, with the exception of arriving and parallel shores during spring. Interestingly, arriving shores had less movement in the main direction of migration compared with the parallel shore. The pattern of weaker movement at arriving shores in the main direction of migration may be because of a time lag: at dusk, migrants have not had time to cross the lake and reach arriving shores. Even at a fast ground speed (e.g., 52.46 km/hr, Nilsson et al. 2014), it would take roughly the entire dusk time period to cross the shortest lake crossing in our dataset. Post-hoc tests show that migration in the coastal migratory direction is the same or stronger than water or land movements at parallel shores, suggesting that these movements are consistent with a time lag for migrants.

Our observation that migrants moved toward land at dawn was consistent with previous studies (Diehl et al. 2003, Archibald et

al. 2017, Heist et al. 2018). Terrestrial migrants may make landfall to avoid predation, to rest, and/or to forage and replenish fat stores, and migrants appear to be unwilling to cross the lakes during daylight. Our findings suggest that landward movements at dawn are found broadly across the Great Lakes, highlighting the importance of shorelines where migrants may be vulnerable to losses of habitat and to collision.

Differences in directional movement among eastern, central, and western Great Lakes

We observed different regional patterns of movement in spring and autumn. Westerly movements on the western edge of the Great Lakes basin and easterly movements on the eastern edge were stronger in spring than in autumn. There are several non-mutually exclusive explanations for the differences in directional movement during spring and autumn migration. First, there may be a lack of data during autumn migration. Our study was limited to the U.S. side of the Great Lakes. During autumn migration, we had relatively few sites at departing shores, which generally provide more information about migrant decision making. At arriving shores, in contrast, migrants have generally already committed to crossing the lake. Additional autumn data collection in Canada on the northern shores of the Great Lakes would provide a more complete understanding of how migrants make migratory decisions.

Second, geography may affect movements. During spring migration, the Great Lakes basin as a whole is roughly wedge-shaped to migrants approaching from the south, and migrants following the shorelines are still making progress in the intended direction of migration. In contrast, autumn migrants that follow the shore could need to cross several lakes, especially on the eastern side of the Great Lakes where skirting around the eastern shoreline of Lake Huron places migrants in the path of Lakes Erie and Ontario.

Third, the conditions of migration during spring and autumn exert different pressures on migrants and could result in different directional movements. During spring, migrants move away from warm weather and food supplies toward areas that are potentially snow-covered and cooler and have less food available. Both male and female migrants may accrue benefits from arriving early to breeding sites in the spring (Forstmeier 2002, Smith and Moore 2005, Kokko et al. 2006). Migrants must balance these benefits

with the risk of making a lake crossing to an unfavorable habitat (e.g., continued snow on the opposite shore). One way to mitigate such risk would be to move along the shore in the direction closest to the main direction of migration, while looking for opportunities to cross later, or to cross at areas that are less risky. During autumn migration, migrants move toward more reliable food sources and shelter, meaning direct crossings may be less risky. Combining radar data with information on age classes and sex of migrants via banding or radiotelemetry could show how migration varies across seasons with species, age, and sex.

Conservation implications

Migrants may be more vulnerable when encountering barriers such as the Great Lakes than during other stages of migration. Migrants spend substantial energy stores flying over water unsuitable for landing and face competition because of an increased concentration of migrants. The migratory movement patterns we describe may provide opportunities to reduce risk to migrants. Accounting for shoreline orientation can more accurately predict migrant directional movement at night than using only the main direction of migration. In particular, we would expect a greater proportion of migrants at departing and parallel shores to follow the shoreline than at arriving shores. Migrants crossing the lakes encounter shoreline dangers (e.g., wind turbines, tall buildings, and communications towers) both when leaving and arriving at land. In contrast, migrants following the shoreline will encounter these same shoreline dangers sequentially, with greater cumulative potential for risk than a simple crossing. Risk avoidance and minimization measures, such as lights out policies, turbine feathering, and lighting changes (Gehring et al. 2009, Federal Aviation Administration 2018, Horton et al. 2019, Loss et al. 2019, Smallwood and Bell 2020) may incur costs and be implemented sparingly. Our results suggest prioritizing departing and parallel shorelines for mitigation measures would be more effective for reducing risk during migration. Additionally, we found evidence that migrants may be more directionally constrained at the edges of the Great Lakes basin, suggesting conservation actions may be more useful on those lakes. We note that this study focuses on behavior, but does not assess the magnitude of migrant activity. Synthesizing both migrant airspace activity and behavior at a basin-wide scale would better inform stopover habitat restoration and enhancement and risk reduction programs to improve migrant success on the Great Lakes basin.

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Appendix 1. Radar site, location, shore orientation, days data collected, and shore angle along with metadata

Please click here to download file 'appendix1.xlsx'.

Appendix 2. Site-Specific raw counts and proportions of directional data used for analysis for Dawn, Dusk and night; averaged proportions used for comparisons among shorelines, cardinal and inter-cardinal proportions. Further raw data can be found at: https://www.fws.gov/radar/documents/data/USFWS_Avian_Radar_Data_v1.3.zip

Please click here to download file 'appendix2.xlsx'.