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Morning flight behavior of nocturnally migrating birds along the western basin of Lake Erie

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ABSTRACT. Many species of birds that normally migrate during the night have been observed engaging in so-called morning flights during the early morning. The results of previous studies have supported the hypothesis that one function of morning flights is to compensate for wind drift that birds experienced during the night. Our objective was to further explore this hypothesis in a unique geographic context. We determined the orientation of morning flights along the southern shore of Lake Erie's western basin during the spring migrations of 2016 and 2017. This orientation was then compared to the observed orientation of nocturnal migration. Additionally, the orientation of the birds engaged in morning flights following nights with drifting winds was compared to that of birds following nights with non-drifting winds. The morning flights of most birds at our observation site were oriented to the west-northwest, following the southern coast of Lake Erie. Given that nocturnal migration was oriented generally east of north, the orientation of morning flight necessarily reflected compensation for accumulated, seasonal wind drift resulting from prevailing westerly winds. However, the orientation of morning flights was similar following nights with drifting and non-drifting winds, suggesting that birds on any given morning were not necessarily re-orienting as an immediate response to drift that occurred the previous night. Given the topographical characteristics of our observation area, the west-northwest movement of birds in our study is likely best explained as a more complex interaction that could include some combination of compensation for wind drift, a search for suitable stopover habitat, flying in a direction that minimizes any loss in progressing northward toward the migratory goal, and avoidance of a lake crossing.

RESUMEN. Comportamiento de vuelo de la mañana en aves migratorias nocturnas a lo largo de la Cuenca occidental del lago Erie

Muchas especies de aves que migran normalmente durante la noche han sido observadas iniciando los llamados vuelos de la mañana durante tempranas horas del día. Resultados de estudios previos han soportado la hipótesis que una función de los vuelos de la mañana es para compensar por la deriva del viento que las aves han experimentado durante la noche. Nuestro objetivo era explorar mas a fondo esta hipótesis en un contexto geográfico único. Determinamos la orientación de los vuelos de la mañana a lo largo de la costa sur de la Cuenca occidental del lago Erie durante las migraciones de primavera de 2016 y 2017. Esta orientación fue comparada con la orientación observada de la migración nocturna. Adicionalmente comparamos la orientación de las aves que iniciaron vuelos en la mañana posterior a noches con vientos a la deriva con las de aves después de noches sin vientos a la deriva. Los vuelos de la mañana de la mayoría de las aves en nuestro sitio de observación estuvieron orientados hacia el oeste-noroeste, siguiendo la costa sur del lago Erie. Dado que la migración nocturna fue orientada generalmente al este del norte, la orientación de los vuelos de la mañana necesariamente reflejan compensación por la acumulación de la deriva por los vientos estacionales resultado de vientos principalmente hacia el oeste. Sin embargo, la orientación de los vuelos de la mañana fue similar posterior a noches con vientos de deriva a las noches sin vientos de deriva, sugiriendo que las aves en una mañana cualquiera no necesariamente estaban re-orientándose como respuesta inmediata a la deriva ocurrida la noche anterior. Dadas las características topográficas de nuestra área de observación, los movimientos hacia el oeste-noroeste de las aves en nuestro estudio están mejor explicadas por una interacción mas compleja que puede incluir una combinación de la compensación por la deriva por el viento, una búsqueda de hábitats de parada adecuados, vuelos en una dirección que minimiza la pérdida del progreso norte hacia el objetivo migratorio y evitar cruzamientos del lago.

Key words: geographic barrier, migratory orientation, stopover ecology, topography, wind drift

Many nocturnal migrants make additional movements during the morning hours in a phenomenon called “morning flight” (Baird

and Nisbet 1960, Gauthreaux 1978, Bingman 1980, Yaukey 2010, Van Doren et al. 2015, 2016). Morning flights are most commonly observed near coastal areas, where they are usually directed either toward the coast when

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migrants are over water or inland away from the coast. These coastal morning flights may be oriented in the opposite direction of the nighttime orientation of migrants, allowing them to reach land using the shortest route (Myres 1964, Diehl et al. 2003, Archibald et al. 2017). In addition to returning to land, coastal morning flights, especially along the Atlantic coast of North America, may allow birds to compensate for wind drift accrued during the night; drift that either took the birds out to sea or displaced them from suitable stopover habitat (Baird and Nisbet 1960, Van Doren et al. 2015). However, morning flights are not limited to coastal areas (Gauthreaux 1978, Bingman 1980, Hall and Bell 1981, Yaukey 2010). At some inland locations, the orientation of morning flights has been found to be orthogonal, or nearly so, to the direction of nocturnal flights (Gauthreaux 1978, Yaukey 2010, Van Doren et al. 2015) and, therefore, such flights may serve to compensate for wind drift accrued during the night (Gauthreaux 1978, Van Doren et al. 2015, 2016). At other inland locations, however, the orientation of morning flights has been found to be generally aligned with that observed at night and has been interpreted as advancing the progress of migration while also allowing birds to search for suitable stopover habitat (Bingman 1980, Hall and Bell 1981, Van Doren et al. 2015).

Local topography can influence the orientation of nocturnal migrants (Bingman et al. 1982, Åkesson 1993, Bruderer and Liechti 1998). Whether or not local topography influences morning flight orientation is less well understood, but some support for this idea has been reported (Bingman 1980, Yaukey 2010, but see Hall and Bell 1981). In this study, we were interested in examining the orientation of morning flights at the boundary of a large inland (non-oceanic), topographic barrier: the shore of the western basin of Lake Erie in Ohio, which allowed us to address two deficiencies in the literature. One was to further document the orientation of morning flights at an inland site and, second, to determine if orientation by migrants during the morning is influenced by large topographic barriers as it seems to be at night. Although Lake Erie is an imposing topographic barrier, migrants routinely cross it at night (Diehl et al. 2003, Gesicki et al.

2016) and, from our observation site (see below), coastal Michigan can be seen to the north. Therefore, flying north over the lake during the morning was a feasible orientation option. Our objective was to document the occurrence, taxonomic composition, and orientation of morning flights on the Lake Erie's southern coast during spring migration. In the context of the topographic barrier of the lake, we were further interested in determining if the orientation could be functionally interpreted as a corrective response to wind drift or a continuation of nocturnal migration, and the extent to which searching for suitable stopover habitat may have motivated the morning flights.

METHODS

We observed morning flight behavior along the southern shore of Lake Erie at the Ottawa National Wildlife Refuge, Oak Harbor, Ohio, USA (41°38'18"N, -83°12'54"W; Fig. 1). The sampling site was located along a gravel dike that extended from the southeast to the northwest and was bordered by Lake Erie to the northeast and a shallow impoundment wetland mixed with small patches of hardwood trees to the southwest. Lake Erie's coastal marshes and associated beach-ridges provide rich stopover habitat for Neotropical migrants, including warblers (Parulidae), vireos (Vireonidae), and flycatchers (Tyrannidae). During the springs of 2016 (18 April–29 May; 18 mornings with at least one morning flight observation) and 2017 (9 April–2 June; 20 mornings with at least one morning flight observation), we determined the orientation of morning flights and identified birds making those flights to at least the family level. Observations took place for 2 h starting at sunrise and coincided with the peak of morning flight behavior (Wiedner et al. 1992). Visual scans overhead and along the horizon were conducted every 2 min. Birds were visually spotted or alerted to by calls. Migrants were considered to be engaged in morning flight if observed above canopy height and tracked flying in a straight line before disappearing on the horizon. We followed birds using 8 × 42 binoculars until they disappeared on the horizon and vanishing bearings were recorded using a hand compass. View of the horizon was unobstructed

in all directions except toward the south where patches of trees were present. Flight directions were later adjusted to reference geographic north based on local magnetic declination. Birds were considered part of a group if one bird was still within sight when a second became visible. Birds observed as a group were recorded as a single independent observation. To prevent errors resulting from parallax, only birds seen moving overhead or within ~ 30 m of the overhead corridor were counted.

Nocturnal orientation, collection, and analysis of Doppler radar and infrared data. For radar data, Level II WSR-88D radar product, radial velocity, was downloaded from the National Centers for Environmental Information (NCEI) (www.ncdc.noaa.gov) for station KILN near Cincinnati, Ohio ($39^{\circ}41'50''\text{N}$, $-83^{\circ}81'70''\text{W}$). KILN was located 250 km south of our morning flight sampling location and was the closest Doppler radar station that captured migrants approaching the southern coast of Lake Erie. Radar profiles corresponding to midnight local time were downloaded for each night preceding mornings when at least one bird was observed in morning flight. Radial velocity is a measure of the mean target velocity relative to the radar. Birds moving toward the radar show negative velocity, whereas those moving away from the radar show positive velocity. Velocity also allows identification of targets captured as either birds or insects. Insects fly at low airspeeds and, as a result, their velocity relative to the radar is close to

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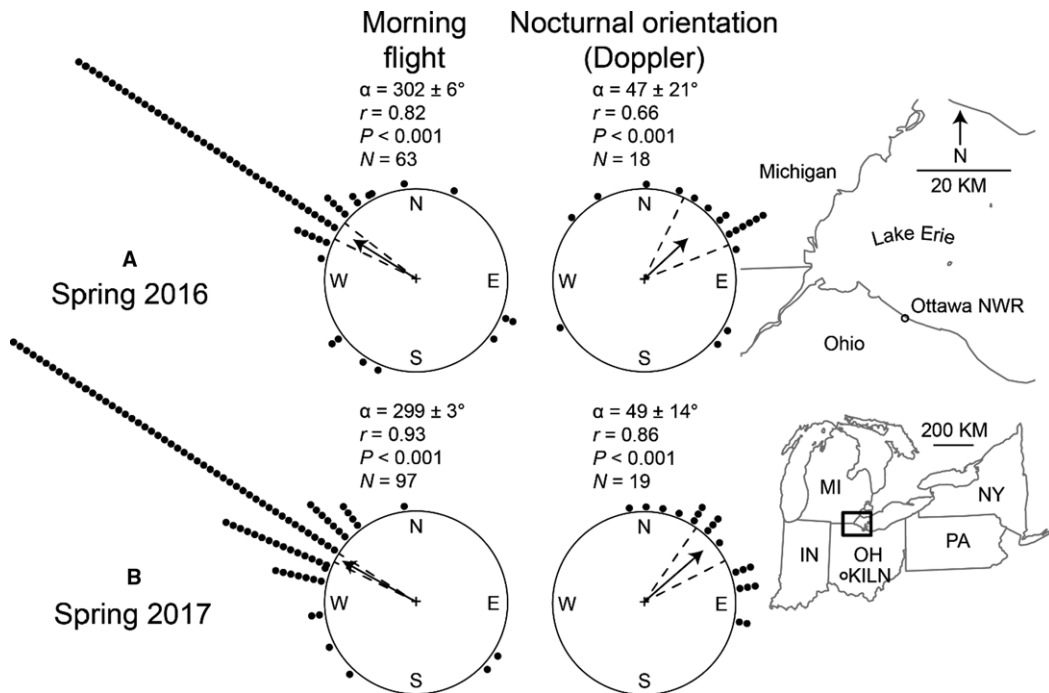


Fig. 1. Circle plots of morning flight and nocturnal orientation (derived from weather surveillance radar station KILN in Cincinnati, Ohio; see location on bottom inset map of the eastern Great Lakes region) from (A) spring 2016 and (B) spring 2017. The black arrows display the overall mean direction of a distribution, the length of arrows corresponds to the length of the mean vector (r) with 0 at the origin and 1.0 equal to the circle radius, and the dashed lines are 95% confidence intervals. Each dot at the periphery of a circle identifies either the orientation of one independent morning flight observation or the nightly mean orientation recorded near Cincinnati. α , mean direction (with 95% confidence intervals), r , mean vector length, and P , significance level based on Rayleigh test. Top inset map of the morning flight observation site along the southwestern edge of Lake Erie at Ottawa National Wildlife Refuge, Oak Harbor, Ohio, contextualized within the eastern Great Lakes region (highlighted box in bottom inset).

the general speed and direction of winds aloft (Larkin 1991). For migrating birds, velocity values can approximate the general, broad-front direction they are moving. We used a Matlab program written by Daniel Sheldon at The University of Massachusetts Amherst to analyze radar profiles to produce velocity azimuth display (VAD) profiles (Sheldon et al. 2013, Farnsworth et al. 2014, Sheldon 2015). The VAD profile gives an average ground speed and track direction of flight for migrants at different altitudinal bands around the radar station. We used the mean track direction corresponding to an altitude of 600 m as an estimate of a given night's broad-front direction. Mean peak nocturnal migration moving through the Great Lakes has been observed at 500–600 m (Archibald et al. 2017).

The orientation of nocturnally migrating birds before they reach the count site determined by Doppler radar is crucial in interpreting the functional significance of morning flight orientation. However, equally useful is the nocturnal flight direction of migrants at or near the morning flight observation site. A nearby thermal-imaging camera (FLIR SR-19, FLIR Systems, Wilsonville, OR) was operated throughout the night on several nights prior to observed morning flight. Sampling took place on nights with no rain and clear skies. The camera was positioned vertically and oriented to the north using a handheld compass. Flight directions were recorded for all targets with bird characteristics, i.e., distinct pulses of the thermal signature caused by flapping wings, straightness of path, and the duration of the target moving through the field of view. Flight directions were measured visually in degrees with the aid of protractor referenced to magnetic north. Flight directions were later adjusted to reference geographic north based on local magnetic declination. Mean directions were calculated for each night prior to observed morning flight. Thermal-imaging observations were taken at the count site during spring 2016 and, in conjunction with another study, at the nearby Cedar Point Wildlife Refuge (15 km west of the observation site) during spring 2017 (41°42'19"N, –83°20'08"W).

Meteorological data. Wind direction data (we considered wind to occur when speeds exceeded 2 m/s) were downloaded

from the National Oceanic and Atmospheric Administration's (NOAA) North American Regional Reanalysis (NARR) using the grid-cell located nearest to the Cincinnati-area radar (~39.42°N, –83.82°W). Measurements were collected at 23:00 EST, 3:00 EST, and 9:00 EST for each night/morning preceding/during morning flight observations. Mean wind directions across the three sampling times for each night were calculated and used in the wind-effect analyses. Wind for a given night was classified as non-drifting if within 45° of the axis along a season's mean nocturnal direction, as determined from the Cincinnati radar site, using data collected on nights preceding mornings with at least one migrant observed engaged in morning flight. Wind was considered drifting if it fell outside 45° of that axis. The principal axis of the non-drifting winds was generally oriented north-northeast/south-southwest and the principal axis of drifting winds was oriented west-northwest/east-southeast for both seasons (12 of 15 nights with drifting winds had winds coming from the west).

Data analysis. Standard circular statistics were used in the analysis of the orientation data (Batschelet 1981). Circular distributions were tested against uniformity using the Rayleigh test and all between-group comparisons were conducted using the Watson U^2 test. Statistical analyses were conducted using program R package *circular* (R v3.2.1, R Core Team 2015) and Oriana (v4.02, Kovach 2011). Values are provided as means \pm 95% confidence intervals.

RESULTS

We observed 341 nocturnal songbird migrants (138 in spring 2016, 203 in spring 2017; Table 1) making morning flights, with a mean time of occurrence of 1.1 h after sunrise. Of the birds observed, 46% were warblers (Parulidae), 20% were flycatchers (Tyrannidae), and 8% were sparrows (Emberizidae).

Morning flight and nocturnal orientation. The mean orientation of birds during morning flights during spring 2016 was $302 \pm 6^\circ$ (Rayleigh test, mean vector length $r = 0.82$, $P < 0.001$). Most birds were observed moving along the coast to the west-northwest, with 40 of 63 independent

Table 1. Total number of birds observed making morning flights organized by family and species.

Family and species	Spring 2016		Spring 2017	
	Total number	Number of independent observations	Total number	Number of independent observations
Cuculidae				
Unknown cuckoo	1	1	0	0
Trochilidae				
Ruby-throated Hummingbird (<i>Archilochus colubris</i>)	4	3	2	2
Tyrannidae				
Eastern Kingbird (<i>Tyrannus tyrannus</i>)	2	2	36	24
Great Crested Flycatcher (<i>Myiarchus crinitus</i>)	0	0	2	1
Unknown flycatcher	0	0	29	6
Turdidae				
Eastern Bluebird (<i>Sialia sialis</i>)	0	0	2	1
Unknown thrush	1	1	15	3
Parulidae				
Yellow Warbler (<i>Setophaga petechia</i>)	4	2	0	0
Yellow-rumped Warbler (<i>Setophaga coronata</i>)	3	1	0	0
Blackpoll Warbler (<i>Setophaga striata</i>)	0	0	1	1
Unknown warbler	85	36	67	34
Emberizidae				
Unknown sparrow	27	8	1	1
Cardinalidae				
Indigo Bunting (<i>Passerina cyanea</i>)	1	1	2	2
Scarlet Tanager (<i>Piranga olivacea</i>)	3	2	2	1
Icteridae				
Baltimore Oriole (<i>Icterus galbula</i>)	7	6	44	21
Total	138	63	203	97

The total number refers to every individual bird that was observed, whereas number of independent observations refers to the number of independent morning flight directions recorded (see Methods).

observations (63.5%) oriented at 303° (Fig. 1). Mean nightly orientation of nocturnal flights near Cincinnati during spring 2016 was $47 \pm 21^\circ$ ($r = 0.66$, $P < 0.001$). Similarly, mean orientation of birds engaged in morning flight during spring 2017 was $299 \pm 3^\circ$ ($r = 0.93$, $P < 0.001$). Again, during spring 2017, most birds were moving west-northwest along the coast, with 56 of 97 independent observations (57.7%) oriented at 303° . The mean nightly orientation of nocturnal flights near Cincinnati during spring 2017 was $49 \pm 14^\circ$ ($r = 0.86$, $P < 0.001$). The distribution of morning flight directions differed from the nocturnal orientation distribution near Cincinnati during spring 2016 (Watson $U^2 = 0.9$, $P < 0.001$) and 2017 (Watson $U^2 = 1.3$, $P < 0.001$).

A potentially more meaningful analysis would include only mornings with a more substantial morning flight. As such, we chose

mornings with at least four independent observations and this occurred during six mornings in spring 2016, with a mean morning flight direction of $304 \pm 2^\circ$ ($r = 0.99$, $P < 0.001$). By contrast, the mean orientation for the six corresponding nocturnal migrations was 30° ($r = 0.61$, $P = 0.108$). In spring 2017, at least four independent morning flight observations were recorded on 10 mornings, with a mean direction of $301 \pm 3^\circ$ ($r = 0.99$, $P < 0.001$). The mean orientation for the 10 corresponding nocturnal migrations was $34 \pm 17^\circ$ ($r = 0.89$, $P < 0.001$). Data from mornings with at least four independent observations were consistent with those when all mornings and their corresponding nights were analyzed (Fig. 1). Orientation on mornings with at least four independent observations was significantly different from the nocturnal orientation of migration over Cincinnati during spring 2017

(Watson $U^2 = 0.43$, $P < 0.001$). No comparison was made for 2016 because the distribution of the nocturnal orientation did not differ from uniform.

Comparisons between the morning flight orientation and nocturnal orientation were potentially confounded by the 250 km that separated our morning flight observation site and the Cincinnati radar station. To complement this analysis, we compared morning flight orientation and the direction of nocturnal migration at or near the count site the previous night. The pooled 2016–2017 mean morning flight orientation for the 10 mornings following nocturnal monitoring using thermal-imaging cameras and with at least four independent morning bearings recorded was $301 \pm 3^\circ$ ($r = 0.99$, $P < 0.001$, Fig. 2), whereas the mean flight direction for the 10 corresponding nights was $351 \pm 9^\circ$ ($r = 0.97$, $P < 0.001$, Fig. 2). This difference was statistically significant (Watson $U^2 = 0.42$, $P < 0.001$). Although the IR-recorded local, nocturnal orientation was more northerly than that recorded by radar, qualitatively similar differences between

nocturnal and morning flight orientation were still readily demonstrated.

Wind and the orientation of morning flights. Of 61 independent morning flight observations during spring 2016, 38 followed eight nights with drifting winds (mean orientation = $306 \pm 7^\circ$, $r = 0.75$, $P < 0.001$) and 25 followed 10 nights with non-drifting winds ($297 \pm 6^\circ$, $r = 0.93$, $P < 0.001$, Fig. 3). Morning flight directions following nights of drifting and non-drifting winds did not differ (Watson $U^2 = 0.14$, $P = 0.30$). We observed 97 independent morning flights during spring 2017, 59 followed seven nights with drifting winds (mean orientation = $300 \pm 4^\circ$, $r = 0.92$, $P < 0.001$) and 38 followed 13 nights of non-drifting winds ($299 \pm 3^\circ$, $r = 0.93$, $P < 0.001$). As in 2016, mean morning flight directions following nights of drifting and non-drifting winds did not differ (Watson $U^2 = 0.04$, $P = 0.67$). However, our analysis does indicate that morning flights were more pronounced on mornings following nights with drifting winds than on mornings following non-drifting winds; 97 morning flight bearings were recorded after 15 nights of drifting winds and only 63 morning flight bearings were recorded after 23 nights of non-drifting winds.

Van Doren et al. (2015) reported that the magnitude of morning flights was greater following nights with higher cross (drifting) wind speeds than nights with weaker crosswinds. We therefore conducted a regression analysis to determine if the number of birds observed on mornings after nights with westerly drifting winds correlated with the strength of those crosswinds. No correlation was found ($N = 12$, $F_{1,10} = 0.4$, $P = 0.56$, $r^2 = 0.03$). However, our sample size was substantially smaller than that of Van Doren et al. (2015) and we had no mornings that followed a night with strong crosswinds (> 10 m/s). On the one morning following reasonably strong crosswinds from the west (9.7 m/s), only one morning flight observation was recorded.

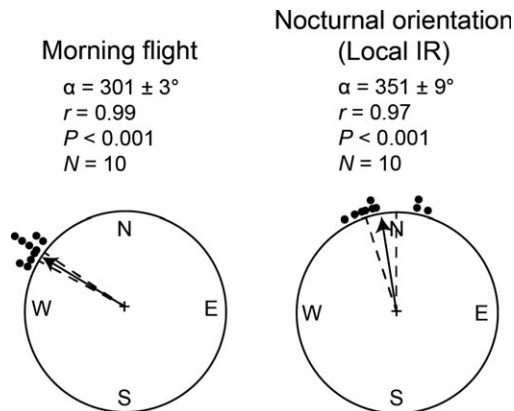


Fig. 2. Circle plots of morning flight orientation and nocturnal migratory direction derived from a thermal-imaging camera operated at or near the morning flight observation site. Dots on the periphery of a circle identify either the mean morning flight direction for a morning with at least four independent observations (morning flight) or the mean direction of nocturnal migration recorded on a previous night (Nocturnal orientation). See Fig. 1 for an explanation of the remainder of the figure.

DISCUSSION

Morning flights by spring nocturnal migrants at our observation site on the southern shore of Lake Erie were overwhelmingly

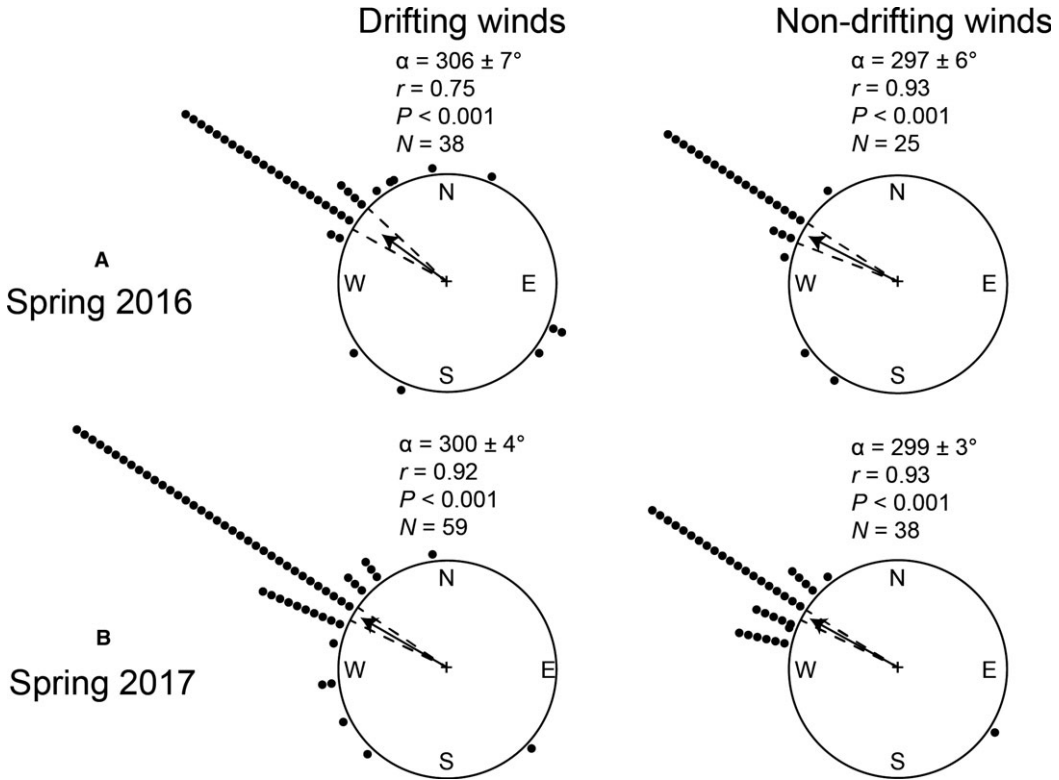


Fig. 3. Circle plots of morning flight directions following nights with drifting winds compared to those following nights with non-drifting winds during (A) spring 2016 and (B) spring 2017. See Fig. 1 for an explanation of the remainder of the figure.

oriented along the coastline to the west-northwest. The influence of the local topography of the Lake Erie coast on morning flight orientation could not be clearer, but its functional significance is less obvious. The prevailing view of morning flights is that they allow birds to compensate for the drifting effects of winds experienced at night (Gauthreaux 1978, Van Doren et al. 2015, 2016), and our data were generally consistent with this interpretation. The principal direction of nocturnal migration in the Great Lakes region is either to the north or north-northeast (Diehl et al. 2003, our study) and drifting winds are almost exclusively from a westerly direction. In our study, drifting winds were from the east on the previous night on only three of 15 mornings and, even on those three mornings, the orientation of the few birds observed was still along the coast to the west-northwest. Given that the orientation of morning flights to the west-northwest is generally

orthogonal to the principal direction of nocturnal flights and toward the direction of the primary source of drifting winds, the observed morning flights were necessarily corrective for at least seasonally accumulated wind drift (see also Gauthreaux 1978).

Van Doren et al. (2015, 2016) suggested that morning flights in their study areas on the coast of the Mid-Atlantic States and inland New York and Pennsylvania may have been a response to drift experienced the previous night. Moore (1990) similarly found evidence of compensation for the previous night's drift in captive migrants. However, that did not seem to be the case at our study site on the coast of Lake Erie. Although our sample sizes were smaller than those of Van Doren et al. (2015, 2016), we found no difference in the orientation of morning flights on mornings following nights with drifting and non-drifting winds, and our modest analysis revealed no previous-night wind-speed

effects (looking at westerly crosswinds only) on morning flight volume. Although the observed orientation of songbirds at Ohio's Lake Erie coast in the morning would necessarily be compensatory for accumulated, seasonal wind drift, the flights did not appear to be an immediate response to the effect of wind during the previous night.

Migrants in our study did not cross Lake Erie in the morning and the orientation of their flights paralleling the coastline could be interpreted as the birds simply responding to the coastline, with any potential consequence with respect to compensating for wind drift being incidental. Other investigators have also reported cases where morning flight orientation was influenced by local topography (Bingman 1980 and, to a lesser extent, Hall and Bell 1981). However, if simply following a coastline to avoid a lake crossing, birds in our study should have also been observed flying along the coast to the east-southeast. Given that we observed no birds flying to the east-southeast, factors other than avoiding a lake crossing may have contributed to the apparent preference for birds to fly west along the coast. For example, a west-northwest movement would allow birds to advance the progression northward to their migratory goal, or at least not result in as much distance lost as would be more likely with an east-southeast movement. Also, the horizon to the west would have been dominated by land (Lake Erie narrows to the west), an attraction with the potential for locating more suitable stopover sites.

In summary, the hypothesized benefits of morning flights are generally considered to be some combination of compensation for wind drift, advancing migration toward its goal, and searching for suitable stopover sites (along oceanic and other large body coastlines a further benefit would be returning to land). Minimally, morning flights near the southern shore of Lake Erie's western basin necessarily provide two of those benefits: compensation for seasonally accumulated wind drift and the search for suitable stopover sites. However, given the topographical characteristics of our observation area, the west-northwest movement in our study is likely best explained as a more complex interaction that includes some combination of compensation for wind drift, a search for suitable stopover habitat, flying in a direction that minimizes any loss in

progressing northward toward the migratory goal, and avoidance of a lake crossing.

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