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RESEARCH ARTICLE

Autumn morning flights of migrant songbirds in the northeastern United States are linked to nocturnal migration and winds aloft

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ABSTRACT

Many passerines that typically migrate at night also engage in migratory flights just after sunrise. These widely observed "morning flights" often involve birds flying in directions other than those aimed toward their ultimate destinations, especially in coastal areas. Morning flights have received little formal investigation, and their study may improve our understanding of how birds orient themselves during and after nocturnal movements and how they use stopover habitat. We studied autumn morning flights in the northeastern United States to identify associations between the number of birds undertaking morning flights and the magnitude of nocturnal migratory movements, nocturnal winds, and local topography. Our analyses included observations of more than 15,000 passerines at 7 locations. We found positive relationships between morning flight size and nocturnal migration density and winds aloft: Significantly more birds flew following larger nocturnal movements, quantified from weather surveillance radar and recordings of nocturnal flight calls, and after stronger nocturnal crosswinds. We also found consistent differences in morning flight size and direction among sites. These patterns are consistent with migrants engaging in morning flight as a corrective measure following displacement by nocturnal winds and to search for suitable stopover habitat.

Keywords: morning flight, migration, nocturnal migration, stopover, redetermined migration, passerines, Doppler radar, flight calls

Los vuelos matutinos de las aves migratorias en otoño en el noreste de Estados Unidos se relacionan con la migración nocturna y los vientos de altura

RESUMEN

Muchas aves paserinas que normalmente migran en la noche también pueden hacer vuelos migratorios justo después del amanecer. Estos 'vuelos matutinos' han sido ampliamente observados y generalmente involucran a aves que vuelan en direcciones diferentes a las de sus destinos finales, especialmente en áreas costeras. Los vuelos matutinos han sido poco investigados formalmente, a pesar de que su estudio puede mejorar nuestro entendimiento sobre cómo se orientan las aves durante y después de los movimientos nocturnos, y sobre el uso de hábitats de parada migratoria. Estudiamos los vuelos matutinos en la migración de otoño en el noreste de Estados Unidos para identificar asociaciones entre el número de aves que hacen vuelos matutinos y la magnitud de los movimientos migratorios nocturnos, los vientos nocturnos y la topografía local. Nuestros análisis incluyen observaciones de más de 15000 aves paserinas en siete localidades. Encontramos relaciones positivas entre la cantidad de aves que hacen vuelos matutinos y la densidad de aves durante la migración nocturna y los vientos de altura: significativamente más aves volaron en la mañana luego de movimientos nocturnos con alto número de individuos (cuantificados mediante radares de vigilancia climática y grabaciones de llamados nocturnos de vuelo) y luego de fuertes vientos nocturnos en contra. También encontramos diferencias consistentes en el tamaño de los grupos de vuelo matutino y en la dirección entre sitios. Estos patrones concuerdan con la idea de que las aves migrantes hacen vuelos matutinos como medida correctiva posterior al desplazamiento por vientos nocturnos y a la búsqueda de hábitat de parada adecuado.

Palabras clave: llamados de vuelo, migración, migración redeterminada, migración nocturna, paserinos, radar Doppler, sitios de parada migratoria, vuelos matutinos.

INTRODUCTION

Although songbirds are primarily active during daylight hours for much of the year, many undertake long-distance migratory flights during the night in spring and fall (Wetmore 1926, Lowery and Newman 1955, Newton 2008). Migrating during the night is advantageous for small birds because they maximize daylight foraging time, benefit physiologically from cooler nocturnal temperatures, fly through a generally less turbulent atmosphere, and experience a decreased risk of predation by bird-eating diurnal raptors (Brewster 1886, Kerlinger and Moore 1989, Alerstam 2009, but see Ibáñez et al. 2001). Nevertheless, many nocturnally migrating species can also regularly be seen moving in the early daylight hours during migration periods. Such "morning flights" begin near sunrise and generally consist of songbirds flying above tree height in a directional manner, singly or in loose groups, often while uttering "flight call" vocalizations typically given during nocturnal migration (Baird and Nisbet 1960, Bingman 1980, Wiedner et al. 1992, Evans and O'Brien 2002, Farnsworth 2005).

Some morning flights, especially those occurring far inland, appear to consist of birds continuing largely in the direction in which they move at night (Bingman 1980, Hall and Bell 1981). Reported passage rates at inland locations often are smaller than those at coastal sites (e.g., Bingman 1980), although geographic features such as ridgelines appear to concentrate migrants, occasionally resulting in impressive inland flights (Hall and Bell 1981). However, many postsunrise flights of typically nocturnal migrants are not simple continuations of a previous night's migration. Instead, birds may travel in what seem to be seasonally inappropriate directions, including toward the north and west during otherwise southbound autumn movements in the northern hemisphere (Baird and Nisbet 1960, Wiedner et al. 1992, Yaukey 2010). These flights, which can be conspicuous in coastal areas, are termed "redetermined" flights because birds often follow a heading different from that of nocturnal migration (Lack and Williamson 1959, Gauthreaux 1978, Evans and O'Brien 2002). Despite being widely observed, the precise function of nocturnal migrants' morning flights has not been clearly established. Previous studies of morning flight have been at single locations, with potential biases arising from local topography or regional geography on directions and sizes of flights. Additionally, different protocols among these studies for collecting data pose difficulties for synthesis. Thus, no study has yet investigated the relationship between morning flight and nocturnal migration at the regional scale necessary to identify general predictors of morning flight behavior.

Morning flights not oriented in the direction of nocturnal migration may serve to correct for any wind drift experienced while migrating during the previous night. In addition, morning flights may facilitate proper habitat selection. This is critical for all recently arrived nocturnal migrants, who must refuel during the day (Alerstam 1978, Lindström and Alerstam 1986, Wiedner et al. 1992, Moore et al. 1995). The capacity of passerines to correct for wind drift during active nocturnal migration is not entirely clear. Some evidence suggests that migrants can at least partially compensate, especially in the presence of an obvious topographical leading line (e.g., the coast; Åkesson 1993). However, over open water and over inland areas unmarked by major topographical features, passerines are likely to be swept off course by strong winds (Bingman et al. 1982, Liechti 2006). For example, Bingman et al. (1982) found that nocturnal migrants flying over inland New York State preferred to head southwest, but were swept coastward when crosswinds from the west and northwest occurred. Morning flight may allow birds to reorient and compensate for such lateral displacement (Baird and Nisbet 1960, Able 1977, Gauthreaux 1978, Moore 1990, Wiedner et al. 1992, Tracey and Greenlaw 2011). An extreme case would be migrants that inadvertently find themselves displaced over open water at dawn and have to reach land before they can rest for the day. This occurs off the Atlantic Coast (e.g., Richardson 1978a) and over the Great Lakes (Diehl et al. 2003). Alerstam (1979) theorized that migrants could gain a net benefit from riding fast, high-altitude winds and then initiating reorientation flights at lower altitudes to compensate for the associated wind drift. However, few studies have examined the wind drift hypothesis directly by relating the number of birds in morning flight to the extent to which wind would have displaced birds from their intended direction of travel.

Here we report the passage rates and directions of morning flights at multiple sites in the northeastern United States to investigate first whether there is consistent evidence that morning flight is a modified extension of the previous night's migration, and second whether morning flight serves a function of reorientation following wind drift. Using a novel combination of data, which quantifies the magnitude of nocturnal migration and observed morning flight, we compare observed morning flights with the sizes of nighttime migratory flights. First, we test the hypothesis that larger observed morning flights follow nights with larger migratory movements, as estimated from weather surveillance radar and nocturnal flight calls. Second, we test whether morning flight magnitude is larger following nights during which prevailing winds were more likely to cause birds to drift off their intended courses. Third, we look for additional evidence that morning flight functions to reorient birds by contrasting the sizes of morning flights between inland and coastal sites. In coastal areas,

TABLE 1. Descriptions of locations in the northeastern U.S. from which we observed morning flight during autumn 2010 (August to November).

Site	Location	Description
Bedford, NY	41.18°N, 73.69°W	Clearing on wooded ridge overlooking surrounding deciduous forest. Good view to north, east, and south. Site 230 m above sea level.
Greenwich, CT	41.10°N, 73.69°W	Mowed lawn and meadow on hilltop, facing east. Good view to north, east, and south; view obstructed to west. Site 152 m above sea level.
Ithaca, NY	42.53°N, 76.55°W	Small peninsula on eastern shore of Cayuga Lake, facing west. Good view to north, west, and south; partial view to east. Lakeshore runs from NNW to SSE. Site 116 m above sea level.
Kunkletown, PA	40.83°N, 75.45°W	Ridgetop meadow surrounded by large deciduous forest. Good view of sky to north, south, and east; partial view to west. Kittatinny Ridge (major Appalachian ridge) to south. Site 281 m above sea level.
Manhattan, NY	40.75°N, 73.96°W	Urban area; rooftop terrace with views in all directions, including view to horizon to the east. Site located ~60 m above sea level.
Robert Moses, NY	40.63°N, 73.22°W	Viewing platform on barrier beach; shore runs east to west. Platform faces south, good views in all directions. Site at sea level.
Rye, NY	40.95°N, 73.70°W	Salt marsh in sheltered harbor. Good view to north, east, and south; nearby forest partially obscures view to west and northwest. Site located <1 m above sea level.

reorientation may be more important due to the proximity of open water. Finally, we compare observations among sites to test for differences in morning flight direction, which would indicate that morning flight is also shaped by local conditions, such as topography and the distribution of available habitat, regardless of broad-scale meteorological and migratory phenomena.

METHODS

Study Area and Scope

We based our analyses on data from multiple sources collected between August 24 and November 8, 2010: direct observations of birds in morning flight, Doppler weather radar (WSR-88D), acoustic recordings, and the North American Regional Reanalysis (NARR; http://www.emc.ncep.noaa.gov/mmb/rreanl/) meteorological dataset generated by the U.S. National Oceanic and Atmospheric Administration (NOAA). Volunteer observers made direct observations of diurnal morning flight at seven locations (Table 1). We chose these sites, located primarily in the New York metropolitan area but also including two sites in inland New York and Pennsylvania, because of their relatively unobstructed views of the surrounding landscape, observer availability, and, in some cases, because of previous anecdotal evidence of concentrated morning flight migration. All observers were skilled at identifying birds in flight. To accommodate scheduling constraints, we collected data on an arbitrary set of days at each site when it was convenient for observers, although we made a concerted effort to synchronize counts on mornings following heavy nocturnal migrations (i.e. when we expected detectable morning flights to occur). Consequently, our data are biased toward days with favorable migration conditions during the previous night, which means that we are likely to have been conservative in our ability to detect factors that affect the intensity of morning flight.

Observation periods began at sunrise and continued for up to 2 hr, depending on flight size and observer availability. We subdivided periods into 15-min segments, during which observers identified every individual migrant in flight as specifically as possible, typically to family or genus, but often to species. Observers recorded directions of flights to the nearest of the eight ordinal directions (i.e. north, northeast, east, etc.). We counted only birds that were in sustained flight and exhibited a directional orientation typical of an active avian migrant. Because this study focused on the links between morning flight and nocturnal migration, we restricted the observational dataset to species that are both known nocturnal migrants and known to engage in "redetermined" morning flights, as classified by Evans and O'Brien (2002). Our goal was to eliminate species that are known to initiate independent migratory movements during crepuscular or daylight hours (i.e. movements in theory unlinked to prior nocturnal migration, often undertaken by icterids, finches, and American Robins (*Turdus migratorius*)).

Observers logged 139.25 total observer-hours during 84 observation periods, covering 49 (64%) out of a possible 77 mornings. Eighty (95%) observation periods lasted at least 1 hr, and 53 (63%) lasted 2 hr. Two or more sites reported counts on 21 (43%) of those 49 mornings, 3 or more on 8 (16%) mornings, 4 or more on 5 (10%) mornings, and 5 sites reported concurrent counts on one morning. Observers recorded a total of 39,638 birds known to be nocturnal migrants in morning flight during the study period, of which we analyzed data from 15,158 individual birds following our inclusion of only species known to make redetermined morning flights.

Weather Surveillance Radar and Winds Aloft

Since its widespread deployment in the late 1990s in the United States, WSR-88D weather surveillance radar (Crum and Alberty 1993) has emerged as an extremely useful tool for tracking bird migration over large spatial extents and at relatively coarse resolution (Gauthreaux and Belser 2003, Chilson et al. 2012a, Kelly et al. 2012). The U.S. National Weather Service allows open access to the products from its radar network. We used the base reflectivity and radial velocity products produced by WSR-88D radars located in Upton, New York, USA (KOKX), Albany, New York (KENX), and Binghamton, New York (KGBM) to determine the magnitude, direction, and speed of bird migration (Gauthreaux et al. 2008).

We quantified the magnitude and direction of autumn nocturnal bird migration by processing raw Level II data from the National Climatic Data Center (NCDC) archive (Crum et al. 1993). For each station, we downloaded one scan per hour from the NCDC archive starting at local sunset and visually screened the scans to reject those containing precipitation or other obvious nonbiological clutter (e.g., due to anomalous propagation). We then employed a set of processing steps summarized below to extract the mean target velocity and bird density for each scan, which we averaged across accepted scans within each night to arrive at nightly measures of bird velocity and relative bird density.

Before processing each scan, we first aligned the radial velocity and reflectivity measurements by placing each onto a fixed three-dimensional polar grid with azimuthal resolution of 0.5°, range resolution of 250 m, and elevation angles of 0.5°, 1.5°, 2.5°, 3.5°, and 4.5°. The portion of the atmosphere represented by one point in this three-dimensional grid is called a pulse volume (PV). We analyzed only those PVs within 37.5 km of the radar station. We applied the technique of Sheldon et al. (2013) to estimate target velocities separately for each elevation bin; these values were later weighted by bird density in the corresponding elevation bins (see below) and then averaged to produce a per-scan target velocity.

For the density calculation, we applied an additional screening step developed by Gauthreaux et al. (2003) to exclude targets with velocities that were too close to the wind velocity and thus may have represented insects or other wind-borne particles. In this step, we analyzed only pulse volumes within 15° of the primary axis of target movement at each 100 m elevation bin above ground level, for which the most accurate airspeed measurements are possible. The method compares the radial velocity in each PV to the radial component of wind velocity in the same PV to determine the target airspeed along the direction of the radar beam, or the "radial airspeed." This value is never greater than the true airspeed, is equal to the true airspeed for targets moving directly toward or away from the radar, and very close to true airspeed for targets with little motion tangential to the radar beam, such as those within the 30° wedge (Gauthreaux and Belser 1998). If the radial airspeed was less than 5 m sec^{-1} (i.e. the PV may have been dominated by slow-moving insects; Larkin 1991, Gauthreaux and Belser 1998, Gauthreaux et al. 2003, Buler and Dawson 2014), the PV was classified as containing nonbird targets and the reflectivity in that PV was set to zero. Our data on wind speed were from NARR, which models wind velocity and direction every 3 hr on a three-dimensional grid of points covering North America. Points were spaced at approximately 32 km intervals in the x- and y-directions and with 29 pressure (elevation) levels. We computed the radial wind velocity for each PV by first extracting the full record of wind velocity and direction from the closest NARR grid point (in space and time) and then computing its component in the direction of the radar beam.

We then calculated bird density in each 100 m elevation bin by averaging the reflectivity values of PVs within 15° of the primary axis of movement in that bin. Any PVs classified as nonbird by the wind-based screening process or with measurements below the signal-to-noise threshold were treated as having zero reflectivity. To mitigate the effect of outliers we discarded the largest and smallest 25% of all values, as well as PVs with very high values (>35 dBZ), prior to computing the average (following Buler and Diehl 2009). Finally, we averaged the per-elevation reflectivity values to obtain the overall reflectivity ($\mathrm{cm}^2\ \mathrm{km}^{-3}$) for a given scan; this is the total effective scattering area of targets (cm^2) per unit volume (km^{-3}; Chilson et al. 2012b) averaged over PVs within 37.5 km of the radar station, hereafter referred to as bird density.

Excluding scans due to precipitation precluded the calculation of bird density for certain nights. However, fewer birds migrate in adverse conditions, especially at times of heavy rain (Gauthreaux 1971, Newton 2007, Hein et al. 2011), and manual inspection of the radar image could usually determine whether at least some biological targets were present in the atmosphere. Because we could not calculate bird density values for nights with precipitation in the area, we manually assigned a bird density value of zero to nights with moderate-to-heavy rainfall and no observable biological atmospheric targets (i.e. no potential migrating birds). If manual inspection revealed both precipitation and biological targets, we did not assign a bird density value for that scan. Out of 228 possible radar-nights, we could not automatically calculate bird density values for 24 due to precipitation; for 12 of these we manually assigned a bird density value of 0 following the criteria above, and the rest we left as missing data because we could not quantify bird density accurately in these cases.

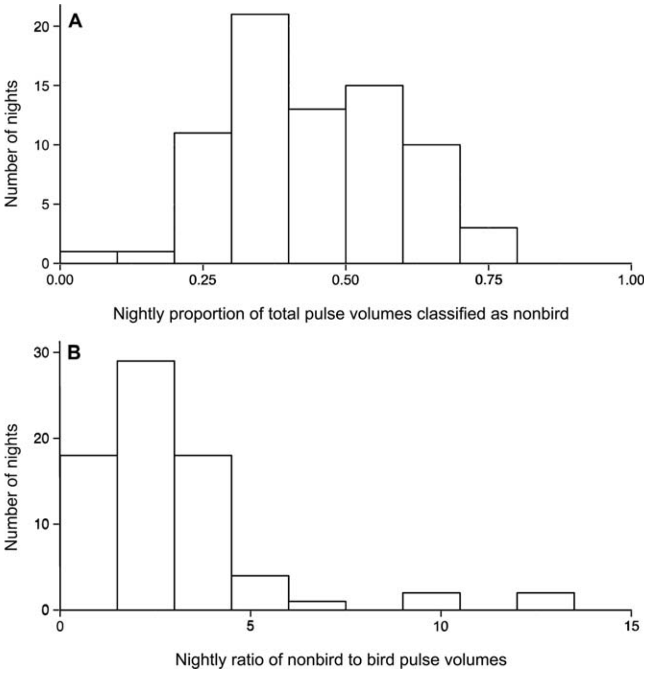

FIGURE 1. Distributions of nightly averages of radar pulse volume classifications in autumn 2010 (August–November) in the northeastern U.S. The pulse volume is a radar sampling unit; one pulse volume is the portion of the atmosphere represented by one point in a fixed three-dimensional polar grid sampled by a radar. Pulse volumes classified as nonbird comprised a substantial portion of many nights' radar scans (**A**), but it was relatively rare that many more pulse volumes were classified as nonbird than bird (**B**). This, in accordance with our sensitivity analysis, suggests that this classification is important for fine-scale quantifications of bird density, but that it may not be as crucial when examining coarse-resolution patterns of nocturnal migration.

To determine the impact on our conclusions of the wind-based screening process for insects and other airborne, nonbird targets, we calculated nightly averages of (1) the proportion of total PVs in each scan classified as wind-borne, and (2) the ratio of the number of wind-borne PVs to the number of bird PVs. During the study period the median proportion of wind-borne PVs per night was 0.46, and the median ratio of wind-borne PVs to bird PVs was 2.59 (Figure 1). This suggests that nonbird targets were present in most radar scans, although we note that two factors limit the accuracy of airspeed estimates and will lead to some fraction of birds being classified as nonbirds: PV-level wind velocities will differ to some extent from the coarser-scale NARR measurements, and some birds within the 30° wedge may deviate from the primary direction of movement and have a lower estimated airspeed due to the greater tangential component of motion. Wind-borne targets dominated (ratio >5 and proportion airborne >0.75) on relatively few nights (Figure 1), but invariably with low overall reflectivity. The nights with the largest average reflectivities (uncorrected for wind-borne targets) had average proportion wind-borne values of approximately 40% of PVs; after screening, these nights also showed large bird movements.

Finally, to determine the sensitivity of our results to possible misclassification of bird vs. nonbird targets, we conducted our model-based analysis (see Statistical Analysis, below) without first filtering by airspeed or restricting to the 30° wedge encompassing the primary direction of movement. Nonetheless, we arrived at the same best model for predicting morning flight observations, showing that the broad patterns of bird migration as they relate to morning flight are qualitatively unaffected by potential misclassification of nonbird targets during the study period.

Nocturnal Flight Calls

Nocturnal flight calls—short flight call notes (<200 ms) regularly uttered during extended migratory flights by many species—provide an additional source of information on the magnitude of overnight migration (see Farnsworth 2005). Because correlations between numbers of flight calls and estimated densities from Doppler radar may not be strong (Larkin et al. 2002, Farnsworth et al. 2004), variation in flight call rates may convey additional behavioral information. For example, birds produce these vocalizations more often when conditions for orientation are poor but winds are still favorable: A low, thick cloud ceiling, thought to impede birds' celestial navigation capabilities, often induces an increase in calling (Farnsworth 2005). Thus, flight call rates may contain information that is relevant to morning flight, such as disorientation and, therefore, potential for wind drift.

We collected recordings of flight calls using Song Meter 2 (SM2, Wildlife Acoustics, Concord, Massachusetts, USA) autonomous recording units (ARUs) deployed at four locations in the New York metropolitan area (Rye, New York; Greenwich, Connecticut; Yonkers, New York; and Bedford, New York) between August 23 and mid-November, 2010. All locations had an unobstructed view of the sky. We preprogrammed each SM2 unit to record uncompressed audio files from the end of evening civil twilight (i.e. when the sun is 6° below the horizon) to 1 hr after sunrise the following morning. For this study, we analyzed recordings only until the beginning of morning civil twilight.

We processed raw recordings using Raven Pro 1.4 sound analysis software (www.birds.cornell.edu/raven). Because flight calls cluster into two distinct groups—higher and lower frequencies—we ran two band-limited energy detector presets on all recordings. The band-limited energy detector identifies signals that stand out from background noise. For higher frequency detections, we used the following settings: 6,000–11,000 Hz frequency range;

TABLE 2. Locations of autonomous recording units used to record morning flight calls of migrant birds in the northeastern U.S. during autumn 2010 (August to November) and summaries of the data collected at each location.

Acoustic site	GPS	Description	Nights recorded (hr)	Total calls
Greenwich, CT	41.10°N, 73.69°W	Meadow with nearby deciduous woods. Unit mounted 1 m above ground level.	71 (792.37)	17,190
Yonkers, NY	40.97°N, 73.88°W	Lawn with nearby deciduous woods. Unit mounted 1 m above ground level.	86 (1010.17)	4,467
Rye, NY	40.96°N, 73.71°W	Large meadow with nearby deciduous woods. Unit mounted 1 m above ground level.	69 (772.57)	3,486
Total			226 (2575.10)	25,143

26.7 msec minimum duration; 400 msec maximum duration; 64 msec minimum separation; 25% minimum occupancy; 3.5 dB signal-to-noise threshold; 4,887.3 msec block size; 245.3 msec hop size; and 50th percentile. For lower frequency detections, settings were largely the same, except for the frequency range, which was 2,500–3,200 Hz. We chose these parameters based on the characteristics of the target calls and the local ambient noise profile, after preliminary work to establish appropriate settings. Band-limited energy detectors may capture 60–96% of calls in recordings, depending on the local ambient noise profile and detector settings (A. Klingensmith personal communication). However, more permissive detection settings also capture large numbers of false positives (e.g., insect noise, rain, and wind), often representing more than 90% of detections (99% in this dataset). Despite the abundance of false detections, which we removed manually, energy detectors substantially decreased the overall amount of work required. One ARU malfunctioned, so we present data from 3 of the 4 deployed ARUs, encompassing 25,143 flight calls (Table 2). Here, we use average nightly call counts (in calls hr^{-1}) as our measure of calling rate. We detected the greatest number of flight calls in the hours preceding dawn, although the temporal calling pattern differed substantially between groups of species (see Figure 2).

Statistical Analyses

Our primary goals were to determine whether the size of morning flights was related to (1) the number of birds migrating during the previous night, (2) the directions of prevailing winds and bird movement during the previous night, and (3) the proximity of an observation site to the coast. Wind conditions strongly affect birds' migration decisions (Richardson 1978b, Gauthreaux 1971, Åkesson and Hedenström 2000, Erni et al. 2005), resulting in correlations among multiple features of weather and the number of nighttime migrants. As a result, our first step was to use principal component analysis to create a small set of predictors of morning flight that were independent of each other.

We assembled a suite of 18 predictors, comprising measures of nocturnal wind, nocturnal bird density and velocity from WSR-88D, and nocturnal flight call rates,

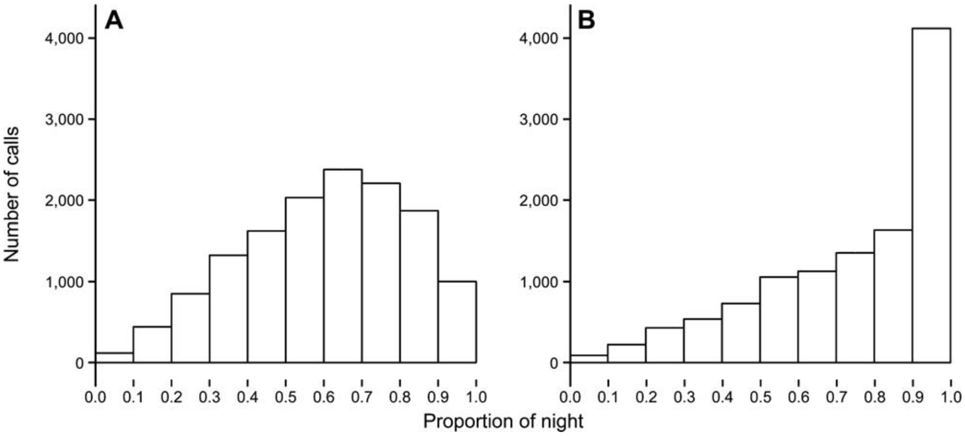

FIGURE 2. Total number of flight calls of nocturnal migrants in the northeastern U.S. recorded at three stations during autumn 2010, by frequency and time of night. Detections of both high frequency calls (**A**) and low frequency calls (**B**) peaked in the hours before dawn. However, recordings of low frequency callers (e.g., thrushes and grosbeaks) peaked in the period immediately before dawn, while recordings of high frequency callers (e.g., warblers and sparrows) peaked between 60% and 65% of the way through the night. The night is defined as the time from the end of civil twilight (dusk) to the beginning of civil twilight (dawn).

TABLE 3. Loading matrix of principal components analysis of 18 predictors. These predictors comprise measures of nocturnal winds, nocturnal bird density and velocity, and nocturnal flight call rate during autumn 2010 (August to November). Radar and wind data correspond to KBGM (Binghamton, NY), KOKX (Upton, NY), and KENX (Albany, NY). Loadings with absolute values >0.60 are in bold font.

Predictor	PC1 (40%)	PC2 (28%)	PC3 (12%)
Nocturnal migration passage rate, KBGM	−**0.80**	−0.10	0.13
Nocturnal migration passage rate, KOKX	−**0.74**	−0.15	0.07
Nocturnal migration passage rate, KENX	−**0.74**	−0.14	0.20
Perpendicular component of nocturnal bird movement, KBGM	0.24	**0.81**	−0.18
Perpendicular component of nocturnal bird movement, KOKX	0.15	**0.87**	−0.02
Perpendicular component of nocturnal bird movement, KENX	0.02	**0.95**	−0.07
Forward component of nocturnal bird movement, KBGM	**0.91**	−0.08	0.21
Forward component of nocturnal bird movement, KOKX	**0.91**	0.15	0.15
Forward component of nocturnal bird movement, KENX	**0.91**	0.03	0.26
Crosswind, KBGM	−0.11	**0.93**	−0.09
Crosswind, KOKX	−0.03	**0.91**	0.07
Crosswind, KENX	−0.31	**0.89**	−0.04
Tailwind, KBGM	**0.77**	−0.03	0.37
Tailwind, KOKX	**0.87**	−0.02	0.22
Tailwind, KENX	**0.86**	−0.06	0.37
Flight call rate: Rye, NY	−0.48	0.23	**0.72**
Flight call rate: Greenwich, CT	−0.49	0.19	**0.73**
Flight call rate: Yonkers, NY	−0.46	0.07	**0.70**

during the period of August 24 to November 7 (Table 3). With NARR data we used nightly mean vectors of 925-millibar nocturnal winds at Binghamton, New York (KGBM), Upton, New York (KOKX), and Albany, New York (KENX), to calculate the tailwind and crosswind components for birds undertaking nocturnal migration. We used the 925-millibar isobar for these measurements because it corresponds well with the altitude at which nocturnal migrants generally fly in North America (see La Sorte et al. 2014). For these calculations we used a heading of 209.7°, the average direction of monthly movement that we detected over the region on Doppler radar during the autumn migration period. Note that this average direction of migration is roughly parallel to the northeastern coast. In the same manner, we calculated the "tail" (i.e. forward movement) and "cross" (i.e. perpendicular movement) components of the nightly mean vector of bird movement on Doppler radar to quantify the extent to which birds deviated from this typical along-coast flight path. To determine the average nocturnal migration traffic rate, we log-transformed the product of nightly bird density aloft and the average target groundspeed. Finally, we included the average number of flight calls recorded per hour from our three listening stations (Table 2). In generating principal components, we used the imputation function in JMP Pro 10 (SAS Institute, Cary, North Carolina, USA) to estimate missing values for 11 of these 18 predictors, with not more than 7% of values estimated for each of 5 predictors and 17–22% estimated for the remaining 6.

Overall, 79% of the variation in these data is represented in three principal components. The first principal component describes the general favorability for southbound nocturnal migration; the simultaneous high factor loading scores for bird density, tailwinds, and nocturnal migration oriented parallel to the coast are consistent with prior knowledge, as southward migratory movements in fall are expected to be highest when assisted by tailwinds. The second principal component describes the potential for wind drift toward the coast, with high factor loading scores for crosswinds and the component of nocturnal migration oriented perpendicular to the typical flight path. The third principal component describes variation in the rate of nocturnal flight calls recorded from our three listening stations.

Because of potential interactions among the conditions described by the principal components, we simultaneously tested whether the number of birds in morning flight was related to general favorability for southbound nocturnal movement (PC1), the potential for nocturnal wind drift toward the coast (PC2), and nocturnal flight call rates (PC3). We constructed linear mixed-effects models (packages lme4 and lmerTest in R; The R Foundation for Statistical Computing, Vienna, Austria) to predict morning flight size, and we included observation site as a random effect in order to account for consistent site-specific variation in the average size of morning flights. To determine whether proximity to the coast described additional variation in morning flight size after accounting for average intersite differences and the effects of weather, we created a categorical variable to describe the coastal proximity of an observation site. We classified a site as "coastal" if a passerine originating at the ocean or sound shore could conceivably fly past it over the course of a morning.

TABLE 4. Summary of mixed-effects model effects predicting daily morning flight size at seven locations in the northeastern U.S. during autumn 2010 (August to November), with the final set of fixed effects determined by a backward stepwise process. All interaction terms showed a significant association with log-transformed morning flight size. Parameter estimates indicate that larger morning flights were associated with conditions generally favorable for typical nocturnal migration (more negative values of PC1) and the capacity for coastward wind drift (higher positive values of PC2). The significant interaction terms indicate that these effects were much reduced at inland sites (see Figure 4). Observation site was included as a random effect to account for significant average differences in morning flight sizes among sites.

Fixed effects	Estimate	SE	df	*t*-value	*P* ($>\|t\|$)
Effect					
(Intercept)	1.94	0.66	8.42	2.93	0.02
PC1	−0.11	0.10	78.80	−1.14	0.26
PC2	0.18	0.14	76.58	1.28	0.21
Coast/Inland	0.50	0.78	8.47	0.63	0.54
PC1 × Coast/Inland	−0.46	0.12	79.35	−3.74	<0.001
PC2 × Coast/Inland	0.44	0.17	77.33	2.60	0.01
PC1 × PC2	0.10	0.04	76.74	2.63	0.01

Random effects	χ^2	χ^2 df	*P*-value
Effect			
Observation site	22.2	1	<0.001

This criterion described all sites except Kunkletown, Pennsylvania, and Ithaca, New York. Hereafter, we refer to this categorical variable as "Coast/Inland." We log-transformed the response variable, the number of birds hr^{-1} in morning flight, because the distribution of the raw birds hr^{-1} data and resulting residuals was highly skewed, an issue that we determined was rectified by the log transformation.

We began with a model that included all three principal components, Coast/Inland, and all possible interactions as fixed effects, and observation site as a random effect. We performed a backward stepwise regression using the "step" function in package lmerTest to identify a candidate for the best model. This function uses *F*-tests of significance to decide whether to retain or eliminate terms. We calculated Akaike's Information Criterion (AIC) scores by optimizing the log-likelihood, not by using the restricted maximum likelihood (REML) criterion, because using AIC enabled more accurate comparisons between models with varying fixed effects.

We recognize that differences in observer skill level and other site-specific characteristics (e.g., elevation and topography) likely contributed to variation in observed morning flight size among locations, and that this may have confounded general comparisons between coastal and inland sites. Fortunately, including observation site as a random effect accounted for some of this site-specific variation. Furthermore, observer skill level was not clustered geographically: There were highly experienced observers both inland (e.g., at Ithaca) and along the coast (e.g., Manhattan). Although we are confident that the patterns revealed in this analysis are not artifacts of observer skill, we interpret the results of this analysis cautiously.

Whereas the majority of our analyses concern numbers of birds in flight, we also tested for the effect of local conditions (e.g., topography) on flight direction, calculating mean flight direction of morning flight at each observation site using a circular average weighted by number of birds. We calculated the 95% confidence intervals of these weighted means from 10,000 bootstrapped samples, with the count of a given taxon per 15-min observation segment considered one observation. In addition, we compared the weighted mean flight directions at each site by calculating 10,000 bootstrapped iterations of the difference in weighted means between each possible pair of sites, rejecting the null hypothesis if zero lay outside the confidence interval. For these 21 comparisons, we used a Bonferroni correction to set our confidence level to 0.0024 (original alpha value of 0.05 divided by 21). For all other statistical tests we used a significance level of 0.05.

We performed all statistical tests in R (R Development Core Team 2013; "Circular" package: Agostinelli and Lund 2011; "lme4" package: Bates et al. 2014; "lmerTest" package: Kuznetsova et al. 2014), except for the principal components analysis, for which we used JMP Pro 10 (SAS Institute, Cary, North Carolina, USA).

RESULTS

Beginning with a model of PC1, PC2, PC3, Coast/Inland, and all possible interactions, we used backward stepwise analysis to identify the best model (Table 4) as the one including PC1, PC2, Coast/Inland, and all pairwise interaction terms for the three remaining main effects. This model had a slightly lower AIC score than the next-best model (AIC = 290.40 compared with AIC = 290.95), which included the additional term of PC3. An analysis-of-

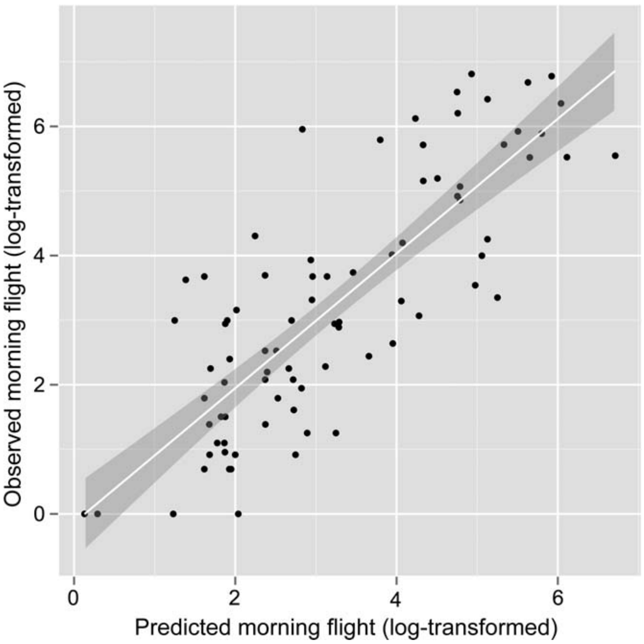

FIGURE 3. Values predicted by the mixed-effects model for the daily number of birds in morning flight in autumn 2010 (August to November) in the northeastern U.S., plotted against observed values. The shaded region represents the 95% confidence interval for this relationship ($R^2 = 0.66$).

variance comparison of these two models indicated that the additional PC3 term did not significantly improve the model ($P = 0.23$), so we used the simpler model in our analysis. This simpler model explained 66% of the variation in observed morning flight size (Figure 3). In this model (Table 4), the estimated coefficients for PC1 ($P = 0.26$) and the PC1 × Coast/Inland interaction ($P < 0.001$) are negative, meaning that tailwinds, greater nocturnal passage rates, and nocturnal migration oriented in the typical direction (largely parallel to the coast) are associated with larger subsequent morning flights. The estimated coefficients for PC2 ($P = 0.21$) and the PC2 × Coast/Inland interaction ($P = 0.01$) are positive, meaning that crosswinds and nocturnal migration oriented perpendicular to the typical direction (largely perpendicular to the coast) are additionally associated with larger subsequent morning flights. Note that in this model only the interaction, not main effects containing PC1 and PC2, are statistically significant. The significant interactions PC1 × Coast/Inland and PC2 × Coast/Inland demonstrate that the effect of weather on morning flight was present at our coastal sites, but was substantially weaker at our inland locations (see Figure 4). That PC3 was not included in the final model indicates that variation in flight call rates did not contribute significantly to explaining morning flight size. Note that the "step" function in lmerTest attempts to

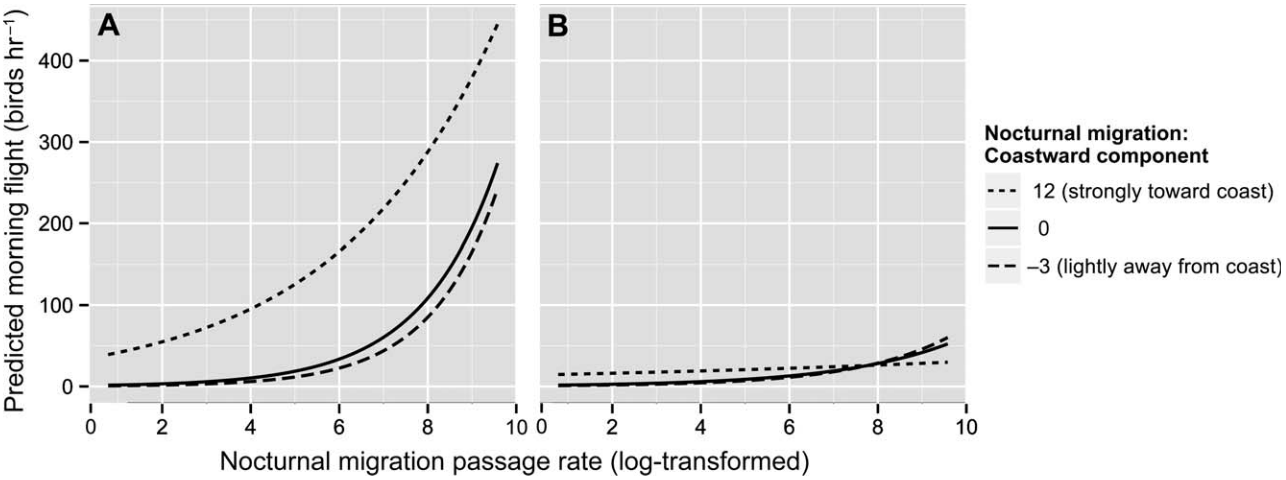

FIGURE 4. Predicted morning flight of "redetermined" migrants in the northeastern U.S. in autumn 2010 (August to November) in coastal (**A**) and inland (**B**) areas, with varying nocturnal winds and bird densities. "Redetermined" migrants primarily migrate at night, but often pursue a heading different from the previous night's in the morning. Because many original predictors were correlated (see Table 3), we replaced principal components here with single original predictors only for illustrative purposes; all correlated variables produced similar illustrations. As conditions for nocturnal migration became more favorable (PC1; represented here by nocturnal migration passage rate) along the *x*-axis, predicted morning flight counts invariably increased. However, the extent of this increase varied greatly depending on coastal proximity and the orientation of nocturnal migration. A greater likelihood of coastward drift (PC2; represented here by the coastward component of nocturnal migration) amplified the effect of migration favorability, while nocturnal migration oriented along the typical axis of movement dampened it. Both effects were substantially reduced in inland areas. The crossed lines at high values of PC1 in inland areas are likely of no biological relevance, but instead an indication that the PC1 × PC2 interaction is shaped largely to precisely characterize the phenomenon at coastal sites, which had larger sample sizes. The range of *x*-values represents the full range of values observed during the study, and the coastward component values of –3, 0, and 12 illustrate the range of variation in the dataset.

TABLE 5. Summary of compass directions and counts of migrating birds in morning flight at all sites in the northeastern U.S. during autumn 2010 (August to November). Means are circular weighted averages across days, with each day's value in the average weighted by the number of birds. The length of the mean vector (between 0 and 1) describes the concentration around the mean, with a value of 1 indicating that all data points lie on the mean direction.

Location	Mean direction	Mean vector length	95% CI of mean direction	Average passage rate (birds hr^{-1} ± 1 SE)
All sites	298.05°	0.66	286.78°, 309.27°	119.2 ± 41.7
Bedford, NY	322.25°	0.67	292.15°, 340.37°	168.0 ± 83.2
Greenwich, CT	342.63°	0.90	332.48°, 351.07°	205.3 ± 67.8
Ithaca, NY	172.12°	0.53	161.11°, 184.28°	8.4 ± 2.4
Kunkletown, PA	290.69°	0.80	282.00°, 299.41°	24.6 ± 8.6
Manhattan, NY	267.02°	0.86	263.86°, 270.06°	306.4 ± 69.3
Robert Moses State Park, NY	272.28°	0.92	271.00°, 274.41°	50.6 ± 22.9
Rye, NY	348.53°	0.87	317.83°, 356.00°	71.3 ± 64.0

remove random as well as fixed effects during backward elimination, and the effect of site-specific variation was statistically strong, thus the random effect was retained in the final model (Table 4).

We also found statistically significant differences in flight direction among sites, indicating the influence of local conditions on morning flight. Weighted circular mean flight directions for all observation sites are shown in Table 5 and Figure 5. All but 5 of the 21 pairwise comparisons made between circular weighted mean flight directions were significant at the Bonferroni-corrected alpha level of 0.0024. The non-significant comparisons are: Bedford-Rye, Bedford-Greenwich, Bedford-Kunkletown, Rye-Kunkletown, and Rye-Greenwich.

DISCUSSION

Morning flight was a salient feature of migrants' movements in our study area, at times in spectacular fashion. Our results allow us to conclude that morning flight and nocturnal migration are significantly related. We found a significant association between PC1, which represents general nighttime migration favorability, and subsequent morning flight size. Although the number and species composition of birds in morning flight clearly represent only a subset of those that moved during the preceding night, our results are consistent with morning flight representing a modified extension of the previous night's migration for these individuals.

Our final model did not include PC3, representing variation in nocturnal flight calls. Although the next-best model did include PC3, which suggests that there may be some relationship between nocturnal flight call activity and morning flight, the high *P*-value (resulting in elimination during stepwise regression) means that this effect is not consistent enough to be statistically significant. Therefore, we suggest that future work on morning flight should continue to examine nocturnal flight calls, even though we did not demonstrate a clear relationship.

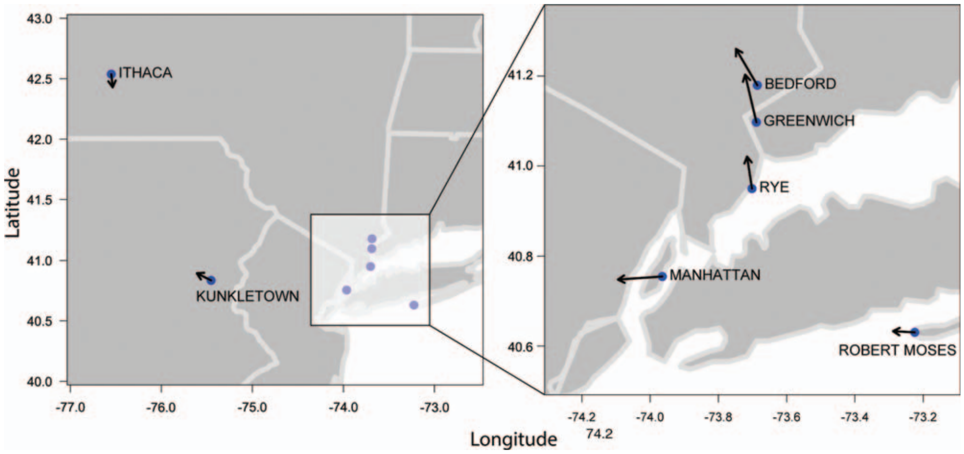

FIGURE 5. Mean flight direction and relative passage rate of migrants at each northeastern U.S. observation location during autumn 2010 (August to November). Arrows point in the mean flight direction of redetermined morning flight migrants (migrants that pursue morning headings different from those of preceding nocturnal migration); arrow length is proportional to the square root of average passage rate. See Table 5 for corresponding values.

Our results suggest that the drive to compensate for wind drift contributes to observed morning flights in concert with the search for appropriate stopover habitat. All migrant songbirds must find suitable stopover habitat, and therefore it is likely that morning-flight migrants are at least partly driven by this need. The additional necessity to compensate for wind drift would be most pressing following conditions conducive to displacement. In the northeastern United States, stronger winds oriented perpendicular to many migrants' typical flight paths (i.e. higher positive values of PC2) describe such conditions. These winds push many migrants to the southeast of their intended flight paths, and this can result in large numbers of displaced migrants in coastal areas and offshore. With stronger crosswinds (higher positive values of PC2), greater numbers of birds are subject to more severe drift, resulting in much larger morning flights at coastal locations (the PC2 × Coast/Inland interaction in Table 4 and Figure 4). Our results show that this phenomenon of general coastward drift described by PC2 is significantly associated with larger morning flights.

Although compensation for wind drift appears to be partially responsible for morning flight, our results indicate that there are other factors at work, related to the locations of sites. Site-to-site variation in the sizes of morning flights can be inferred from published studies of observations at individual sites. For example, Bingman (1980) observed 430 birds (i.e. hundreds of birds) in morning flight near Albany, New York, over the course of a fall season, while coastal studies have observed many tens of thousands (Baird and Nisbet 1960, Wiedner et al. 1992, Yaukey 2010). This previously anecdotal observation was confirmed in our first formal comparison of concurrent morning flights between coastal and inland sites, and in particular by the significant PC1 × Coast/Inland interaction that we found (Table 4, Figure 5). Morning flights were generally larger in coastal areas, despite the fact that nocturnal migratory movements were generally larger farther inland (B. M. Van Doren personal observation). Therefore, the reduced effects of weather and nocturnal migration size at inland sites suggest that migrants may not engage in morning flight as frequently when not near the coast. Although this phenomenon was statistically significant in our model, our sample of inland areas was small ($n = 2$), and future research to confirm the generality of our finding would be useful.

The presence of a significant random effect of site in our final model (Table 4) indicates that we did not measure all relevant factors that affect the size of morning flight at a location. Significant differences in mean flight direction among sites (Table 5) also suggest the additional importance of local conditions, such as topography and variation in the distribution of suitable habitat. In Kunkletown, Pennsylvania, migrants appeared largely to follow an east–west Appalachian ridge. Near Ithaca, New York, where the shore of adjacent Cayuga Lake runs from north–northwest to south–southeast, the mean flight direction was south–southeast. In Greenwich, Connecticut, morning flight was largely directed north–northwest, presumably partly funneled through a valley created by a minor ridge. At Robert Moses, New York, an outer barrier beach runs east to west; morning flight was directed almost exclusively due west along the beach. These patterns are reminiscent of the observations of Wiedner et al. (1992), who noted no day-to-day variation in the direction of morning flights at Cape May, New Jersey; all birds followed the west coast of the Cape May peninsula. Thus, although these comparisons are anecdotal, local bias is probably an important consideration when interpreting the direction of morning flight at any one location, and the effects of topography and habitat on morning flight warrant further exploration.

The question remains whether there exists a single primary purpose for morning flight across the region, in addition to other, important secondary functions. Consistently oriented (albeit generally smaller) morning flights in inland areas (e.g., in Kunkletown and elsewhere in the Appalachians; see Hall and Bell 1981), where suitable habitat is plentiful and located in all directions, imply that migrants are driven by more than stopover habitat location. Furthermore, substantive and well-oriented morning flights at Chestnut Ridge, New York—a "coastal" site, but located several miles inland and surrounded in all directions by suitable stopover habitat—suggest that in coastal areas, too, something other than an early-morning search for a stopover site is at play. Are "coastal" morning flights obligatory drift compensation mechanisms, or a reaction to approaching open water? Birds close to the coast must contend with the unfavorable and proximate ocean, a feature that is not relevant to birds hundreds of kilometers inland. Given the potential dangers of being swept out to sea during their next night of migration, it would make sense for birds that find themselves somewhat near the coast at dawn to move farther inland, independent of any calculated deviation from an intended migratory course. Therefore, there is evidence that multiple factors—the needs to (1) avoid the coast, (2) seek stopover habitat, and (3) reach a migratory goal—may operate together to influence migrants' decisions with respect to morning flight, and that the relative importance of these factors depends on birds' locations and conditions. For example, coastal birds seeking stopover habitat may do so in a direction that also minimizes the danger of flying over water, while inland birds may find it most advantageous to prospect in the seasonally appropriate direction of migration. The smaller numbers of birds observed at inland areas and the differences in the mean direction of flight at observation sites (e.g., Ithaca's southerly direction, compared to the northerly directions at Rye, Greenwich, and Bedford) may reflect the relative importance of these factors. However, further study of these questions would be beneficial, especially a comparison of morning flight behaviors among geographic regions of the eastern United States (e.g., the Appalachian ridges, the Piedmont, and the coastal plain).

Whether migrants undertake morning flight to move away from coastal areas or as a mechanism to correct for wind drift per se, the question remains: Given the benefits of migration by night, why do birds wait until the morning to reorient? Orientation studies, especially in recent years, have implicated cues at sunrise and sunset (e.g., sun azimuth and pattern of light polarization) as the primary signals used by migrating birds to calibrate their internal compasses (Moore 1986, Able and Able 1995, Cochran et al. 2004, Muheim et al. 2006). Because nocturnal migration wanes in the later hours of the night, there appears to be a substantial gap between peak nocturnal migration and peak morning migratory activity (Wiltschko and Höck 1972, Kerlinger and Moore 1989). This is one possible explanation for the difference in temporal flight call patterns between low- and high-frequency callers: High-frequency callers (e.g., warblers and sparrows) may cease their migrations earlier in the night than low-frequency callers (e.g., thrushes), although there is undoubtedly substantial variation among and within species (A. Farnsworth personal observation; Figure 2). We observed a clear lull in bird activity before morning flight began at sunrise, although we did not quantify this phenomenon. At Cape May, New Jersey, large flights commence at sunrise, with limited activity in the preceding minutes; these flights also appear to begin more abruptly on mornings when the disc of the sun is visible, compared with cloudy days (M. O'Brien personal communication). Hall and Bell (1981:136) described a similar phenomenon, remarking, "The beginning of the heavy morning flight is almost as predictable as if it had been programmed by a time clock." Gauthreaux (1978) also reported that redetermined morning flights were greater in number and showed less directional dispersion under sunny skies than in overcast conditions. This raises the interesting possibility that redetermined migrants not over open water may land during the night and await sunrise cues to determine their location with accuracy, after which they may decide whether to undertake corrective measures to find better habitat and/or compensate for wind drift.

Conclusion

Morning flight is an important feature of bird migration. Although the functions of this behavior are not completely understood, we have shown how nocturnal conditions relate to subsequent morning flight and have presented evidence suggesting that migrants engage in these daytime movements at least partially to compensate for wind drift and to locate suitable stopover habitat. We also believe that habitat distribution and local topography may concentrate morning-flight migrants and influence their flight directions; future studies should focus on the role of habitat selection and topography on morning flight behavior. Morning flight is an important factor to consider when studying birds' decisions during migration, including navigation and stopover habitat choice and use. Our results also have implications for conservation, as participation in morning flight can increase birds' risks of exposure to manmade structures (e.g., buildings, communications towers, and wind turbines) and, potentially, aircraft in certain areas.

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