



RESEARCH ARTICLE

Seasonal differences in landbird migration strategies

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ABSTRACT

Migrating birds make strategic decisions at multiple temporal and spatial scales. They must select flight altitudes, speeds, and orientations in order to maintain preferred directions of movement and to minimize energy expenditure and risk. Spring flights follow a rapid phenology, but how this rapid transit translates to in-flight decisions is not clear. We described flight strategies of nocturnally migrating landbirds using 6 weather surveillance radars during spring (2013–2015) and fall (2013–2014) migratory periods in the eastern United States to investigate seasonal decision-making patterns and how climate change may influence these trends. During spring, we found groundspeed and airspeed of migrants to be significantly higher than those of fall migrants; compensation for wind drift was also significantly greater during spring. Our results indicate that birds make more rapid and precise flights in spring that are only partially explained by meteorological phenomena. Future applications at greater spatial scales will allow direct comparisons of in-flight behaviors with predictions from migration theory.

Keywords: aeroecology, bird migration, compensation, NEXRAD, radar, remote sensing, wind drift

Diferencias estacionales en las estrategias de las aves terrestres migratorias

RESUMEN

Las aves en migración toman decisiones estratégicas en múltiples escalas temporales y espaciales. Ellas deben seleccionar la altitud, velocidad y orientación del vuelo para mantener la dirección preferida de movimiento, y para minimizar el gasto de energía y el riesgo. Los vuelos en la primavera siguen una fenología rápida, pero no es claro cómo este tránsito rápido se traduce en decisiones durante el vuelo. Describimos las estrategias de vuelo de aves terrestres que migran durante la noche usando seis radares de vigilancia del clima durante los periodos migratorios de primavera (2013–2015) y otoño (2013–2014) en el oriente de Estados Unidos para investigar los patrones estacionales de toma de decisiones y cómo el cambio climático podría afectar estas tendencias. Encontramos que la velocidad en aire y tierra de las aves migrantes durante la primavera es significativamente mayor que las de la migración de otoño; la compensación por corrientes de viento también fue significativamente mayor durante la primavera. Nuestros resultados indican que las aves hacen vuelos más rápidos y precisos en la primavera que solo pueden ser parcialmente explicados por fenómenos meteorológicos. La aplicación futura de estos métodos en escalas espaciales mayores permitirá comparaciones directas de los comportamientos durante el vuelo con predicciones teóricas de la migración.

Palabras clave: compensación, corrientes de viento, ecología aérea, migración de las aves, NEXRAD, radar, sensores remotos.

INTRODUCTION

The capacity of avian migrants to make time- and place-sensitive decisions in response to seasonal conditions underlies their abilities to successfully reach breeding and wintering grounds (Alerstam 1979, Alerstam and Hedenström 1998). Western hemisphere migratory journeys may span several thousand kilometers, from winter-

ing grounds in Central and South America and southern portions of the United States to northern breeding grounds in the United States and Canada (Newton 2008). Spring migratory movements are generally completed more quickly than fall movements (Newton 2008, La Sorte et al. 2013, 2016, Nilsson et al. 2013). The need for haste in spring is well documented (Newton 2008, La Sorte et al. 2013, Nilsson et al. 2013): birds arriving late to breeding

grounds often suffer reduced fitness (Kokko 1999). However, mechanisms facilitating this increased pace of movement—and how global climate change will influence migration speeds—are less well understood.

Timing differences can stem from variation in stopover behavior and flight strategy. Seasonal differences in stopover behavior have been reported (Morris et al. 1994), but in-flight behaviors remain poorly known, particularly at relevant temporal and spatial extents. Existing natural variation in migration speeds (Bäckman and Alerstam 2003, Nilsson et al. 2013) provides an opportunity to test predictions about the role of in-flight behaviors in determining overall migration speed, defined as the time required to transit between wintering and breeding grounds. Our understanding of the mechanisms that operate en route at the migration assemblage level, such as how migrants actively manage their flight altitude, speed, and orientation, are imperative for forecasting future implications for migratory birds, particularly with mounting evidence that climate change alters migration phenology (Butler 2003, Jonzén et al. 2006).

Prevailing wind conditions and birds' flight strategies, in combination, exert the greatest influence on migration speeds (Kemp et al. 2010, Nilsson et al. 2014), but few studies have examined these factors in North America at an assemblage level (La Sorte et al. 2014). We hypothesize that migrants select flight strategies in spring that facilitate faster migration with increased airspeeds and greater compensation for wind drift (Bäckman and Alerstam 2003, Nilsson et al. 2013). To study these behaviors at large spatial scales, we use recent advances in radar remote sensing (Stepanian and Horton 2015) to measure the aggregated behaviors of millions of individual birds during spring and fall along the east coast of the United States. We examine these patterns at both coastal and inland sites because recent work has shown that in-flight behaviors differ substantially across these regional landscapes (Horton et al. 2016).

METHODS

Weather Surveillance Radar Data

We used level-II weather surveillance radar (hereafter WSR-88D) products from 3 coastal radars and 3 inland radars (Figures 1 and 2). WSR-88Ds sample the airspace every 5–10 min, sequentially scanning at 0.5 or 1.0° azimuthal intervals and collecting data every 250 m in range from the radar. These radars transmit at 10-cm wavelength, peak power of 750 kW, and possess a typical biological range of approximately 80–125 km (Crum and Albery 1993, Gauthreaux and Belser 1998). The National Weather Service (NWS) within the National Oceanic and Atmospheric Administration (NOAA) operates 5 of these radars (KBGM, KCCX, KDIX, KENX, KOKX) and the

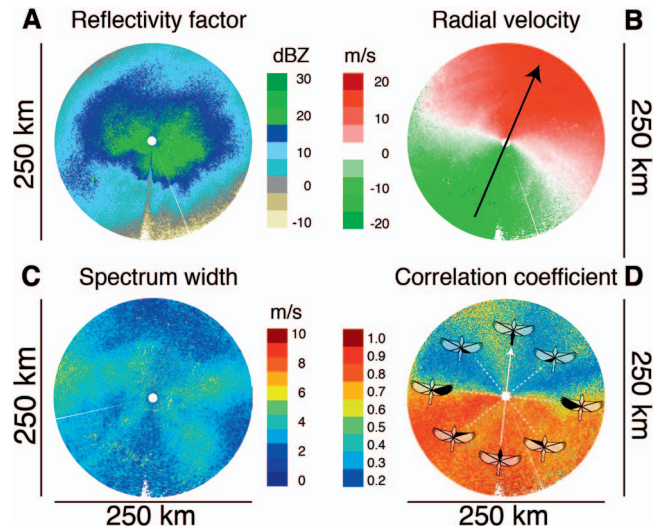


FIGURE 1. Radar measures of (A) reflectivity, (B) radial velocity, (C) spectrum width, and (D) co-polar correlation coefficient from KBGM (Binghamton, NY, USA) for May 4, 2015, 05:33 UTC (~4 hours after local sunset). Radar measures displayed as plan position indicators (PPI) from the lowest elevation sweeps (~0.5°). (A) Reflectivity factor represents general migrant abundance on a logarithmic scale (dBZ). (B) Radial velocity measures migrant groundspeeds approaching (green) and receding (red) from the radar (m s^{-1}), and is used to determine mean track direction (black arrow). (C) Spectrum width measures pulse volume variation in radial velocity (m s^{-1}). (D) Co-polar correlation coefficient is used to measure migrant heading.

Department of Defense (DOD) operates one (KDOX). For low-elevation scans ($<1.5^\circ$), DOD radars sample the airspace at 1.0° azimuthal intervals, rather than the 0.5° intervals that are typical of NOAA operated radars. We downloaded data from these radars from NOAA's National Centers for Environmental Information (NCEI; <http://www.ncdc.noaa.gov/has/has.dselect>) from March 1 to June 15 for spring seasons (2013–2015) and August 1 to November 15 for fall seasons (2013–2014). We retained data between evening and morning civil twilight (sun angle 6° below the horizon), discarding the remaining diurnal data as well as any sweeps containing weather (i.e. contamination from precipitation that obscured bird movements). We summarized radar measures to tenths of the night (i.e. deciles) to control for changes in the duration of nights within and between seasons.

To determine the intensity of migratory movements with respect to height above ground level, we used the 5 lowest-elevation scans from 5 to 20 km to generate vertical profiles of reflectivity at 10-m intervals following Buler and Diehl (2009). For reflectivity averaging we omitted measures with a value of -33 dBZ and values over 35 dBZ to limit clutter contamination. Measures of -33 dBZ represent the minimum detection threshold for WSR-88Ds and are interpreted as having no biological scatters

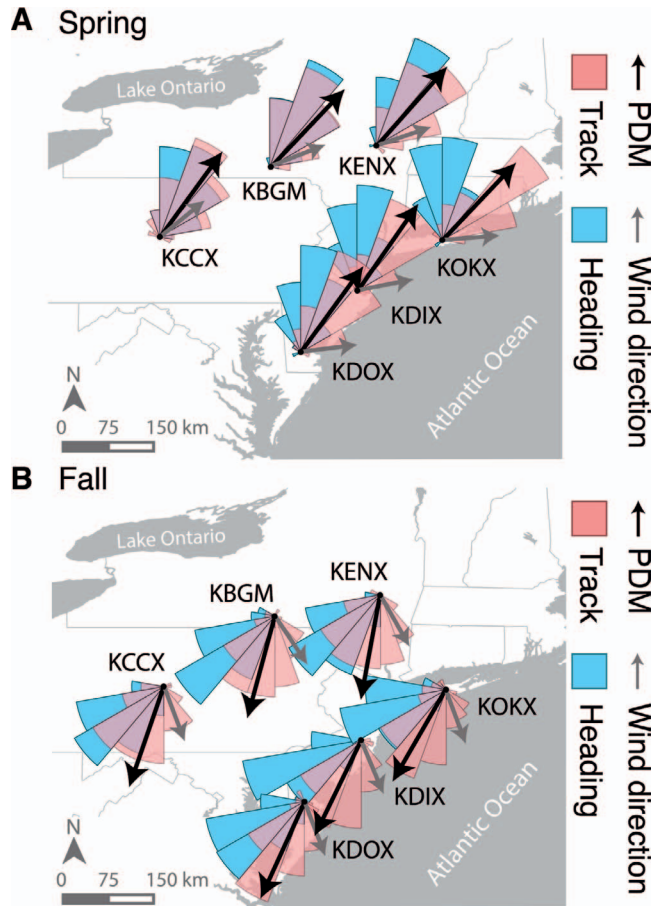


FIGURE 2. Rose diagrams depict distributions of migrant track (red) and heading (blue) for (A) spring and (B) fall migratory seasons. Black arrows denote preferred direction of movement (PDM) and gray arrows mean nightly wind direction. Track and heading distributions were weighted by scaled reflectivity factor, and wind direction by the product of reflectivity factor and wind speed. See Table 1 for site-specific summaries of track, heading, wind direction, and PDM.

(also, termed clear-air). Using the lowest-elevation sweeps ($\sim 0.5^\circ$), we used velocity azimuth display (VAD) techniques on radial velocity fields to determine migrant track, the direction of bird movements over the ground (Figure 1B; Browning and Wexler 1968, Green and Alerstam 2002). When necessary, we dealiased measures of radial velocity (Sheldon et al. 2013). We eliminated VADs with poor fits ($RMSE > 5$), and to limit insect contamination we excluded VADs with $RMSE$ less than one (Dokter et al. 2011). This filtering eliminated 284,429 10-m height bins (11.9%) during spring and 172,100 (5.6%) during fall. The resultant mean $RMSE$ for sites varied from 3.21 and 3.67.

Because radar-derived velocities are an average of behaviors of individuals within a pulse volume, conflicting or diverse migratory strategies within a volume could theoretically be masked, and average airspeed estimates

could be biased low. At times when flight speeds and trajectories within a sampling volume are diverse, we expect the spread, or width, of the Doppler spectrum to be large. Spectrum width is a measure of velocity variability (Figure 1C) that is archived at level-II (Crum and Albery 1993, Crum et al. 1993), but it is used infrequently in biological applications (Diehl and Larkin 2005). To examine the diversity of radial velocities within pulse volumes for evidence that any observed velocity differences could be due to averaging of multiple behaviors, we examined average spectrum width from 20 to 125 km for each sweep. We omitted clear-air measures (i.e. cases with no migration) from these averages.

To determine migrant heading, the direction of the body axis, we used polarimetric azimuth displays (Figure 1D; Stepanian and Horton 2015). In-flight migrants have an anatomical axis of symmetry coincident with their body orientation, and they show strong azimuthal patterns in polarimetric fields (Zrnic and Ryzhkov 1998, Stepanian and Horton 2015). From these data, we defined the axis of symmetry, based on correlation coefficient (ρ_{HV} , Figure 1D; Stepanian and Horton 2015). This axis is the azimuth of orientation of migrants, which is independent of radial velocity and wind measurements.

All measures of migrant track, heading, and ground-speed were projected at 10-m height intervals up to 2 km above ground level. For purposes of averaging we weighted all measures following the distribution of the vertical profile of reflectivity (dBZ).

Winds Aloft

In addition to determining the mean track direction of migrants aloft, VADs also reveal migrant groundspeed (i.e. speed relative to the ground). Groundspeed includes contributions from migrants via powered flight (airspeed) and wind speed and direction. Given estimates of ground-speed, wind direction, and wind speed, we calculated migrant airspeeds through vector subtraction. We used North American Regional Reanalysis (NARR) data to determine wind direction and speed aloft, with a spatial resolution of ~ 32 km and temporal resolution of every 3 hr (Mesinger et al. 2006). For each 10-m measure of groundspeed, we linked the closest spatial and temporal measures of wind speed and direction. As an additional step to limit insect contamination, we eliminated height intervals (10-m samples) with airspeeds less than 5 m s^{-1} (Larkin 1991, Gauthreaux and Belser 1998). This filtering eliminated 118,892 10-m height bins (5.0%) during spring and 335,997 (10.9%) during fall. When summarizing wind vectors we weighted directions by migration intensity (reflectivity) and wind speed (m s^{-1}). To follow the conventions of track and heading directions, we summarized winds to represent the direction toward which winds were moving (Green and Alerstam 2002). In summary, we

apply 2 independent techniques for ameliorating insect contamination in our radar data, filtering by RMSE (Dokter et al. 2011) and airspeeds (Diehl et al. 2003, Buler and Dawson 2014, Van Doren et al. 2014, Horton et al. 2015, Farnsworth et al. 2016), and investigate the seasonal variability in radial velocities using spectrum width. In contrast, most recent radar ornithology studies have applied only one of these methods. Therefore, our dataset is likely to contain less insect contamination than most, if not all, existing studies that have used weather surveillance radar.

Statistics

To determine flight behaviors (i.e. wind drift or compensation), we used a mixed model approach, regressing track on the difference between track and heading (α) (Green and Alerstam 2002). This approach yields 2 important metrics describing migrant flight strategy: (1) slope of α , a measure of drift propensity (0: complete wind drift compensation, 1: complete wind drift); and (2) y -intercept, a measure of preferred direction of movement (PDM) (Chapman et al. 2011, Kemp et al. 2012). To limit pseudoreplication from repeated measure decile samples, we used a series of random effects, including radar site, year, and ordinal date as random intercepts and α as a random slope (Horton et al. 2016, Van Doren et al. 2016). For temporal examinations decile was included as a fixed effect.

We used a linear mixed model (LMM) to test for seasonal and site differences in groundspeeds, airspeeds, and spectrum width, and to calculate radar-specific means of migrant track, heading, groundspeed, and airspeed. We weighted all analyses by scaled radar reflectivity factor (dBZ). We conducted statistical analyses in R, version 3.0.2 (R Core Team 2014), and linear mixed models were implemented using the lme4 and lmerTest packages (Bates et al. 2014, Kuznetsova et al. 2014). We determined the marginal variance explained by fixed effects using the piecewiseSEM package in R (Lefcheck 2015).

RESULTS

Using weather surveillance radar measures (Figure 1A–D) we sampled a total of 67 spring nights (1,756 deciles) and 78 fall nights (2,129 deciles) (Table 1).

Flight Speeds

Migrant groundspeeds were significantly faster during spring (LMM; $P < 0.001$), averaging $4.1 \pm 0.5 \text{ m s}^{-1}$ (mean \pm 95% CI) faster across coastal and inland regions (Figure 3A). Within each season, migrants at inland sites tended toward faster groundspeeds, significantly so only during spring (spring: $1.1 \pm 1.0 \text{ m s}^{-1}$, $P < 0.05$; fall: 0.49

TABLE 1. Sampling effort, mean track, heading, groundspeed, airspeed, wind direction, slope of α , and preferred direction of movement (PDM) for spring and fall migration seasons at six WSR-88D stations in the eastern United States.

Region	Radar	Season	Sampling nights	Deciles	Track (°) \pm 95% CI	Heading (°) \pm 95% CI	Wind (°) \pm 95% CI	Groundspeed (ms^{-1}) \pm 95% CI	Airspeed (ms^{-1}) \pm 95% CI	Slope of α \pm 95% CI	PDM \pm 95% CI
Inland	KBGM	Spring	45	305	36.7 \pm 4.5	34.2 \pm 4.6	68.7 \pm 6.7	14.5 \pm 1.3	10.9 \pm 0.7	0.54 \pm 0.15	44.6 \pm 5.0
		Fall	67	526	194.0 \pm 6.1	233.3 \pm 3.9	146.3 \pm 4.5	11.6 \pm 0.7	8.9 \pm 0.5	0.77 \pm 0.16	195.6 \pm 6.4
	KCCX	Spring	52	376	35.0 \pm 4.5	28.8 \pm 4.5	50.8 \pm 5.9	15.1 \pm 1.2	10.4 \pm 0.7	0.48 \pm 0.15	42.2 \pm 5.0
		Fall	58	445	205.1 \pm 6.2	231.3 \pm 4.0	159.3 \pm 9.6	10.9 \pm 0.7	9.0 \pm 0.5	0.70 \pm 0.16	199.9 \pm 6.4
	KENX	Spring	39	241	47.3 \pm 4.7	33.8 \pm 4.7	71.3 \pm 5.7	15.2 \pm 1.3	9.7 \pm 0.7	0.56 \pm 0.16	49.1 \pm 5.1
		Fall	46	257	196.7 \pm 6.6	226.1 \pm 4.2	150.4 \pm 5.0	11.7 \pm 0.8	8.6 \pm 0.5	0.88 \pm 0.17	191.7 \pm 6.5
Coastal	KDIX	Spring	52	307	40.4 \pm 4.5	3.3 \pm 4.6	79.0 \pm 4.2	14.4 \pm 1.2	10.8 \pm 0.7	0.29 \pm 0.14	35.5 \pm 5.0
		Fall	53	321	201.0 \pm 6.3	245.4 \pm 4.0	157.1 \pm 4.6	10.8 \pm 0.7	8.1 \pm 0.5	0.48 \pm 0.16	206.3 \pm 6.5
	KDOX	Spring	54	329	37.7 \pm 4.5	6.9 \pm 4.5	82.9 \pm 4.9	13.7 \pm 1.2	10.7 \pm 0.7	0.26 \pm 0.14	36.8 \pm 4.9
		Fall	60	359	204.7 \pm 6.1	238.9 \pm 4.0	159.1 \pm 6.2	10.3 \pm 0.7	8.2 \pm 0.5	0.55 \pm 0.16	204.4 \pm 6.4
	KOKX	Spring	37	198	49.6 \pm 4.9	0.7 \pm 4.9	85.6 \pm 5.1	14.0 \pm 1.3	10.4 \pm 0.7	0.33 \pm 0.14	42.4 \pm 5.4
		Fall	38	221	208.1 \pm 6.6	251.2 \pm 4.3	159.5 \pm 5.7	10.0 \pm 0.8	7.6 \pm 0.5	0.50 \pm 0.17	211.0 \pm 6.6

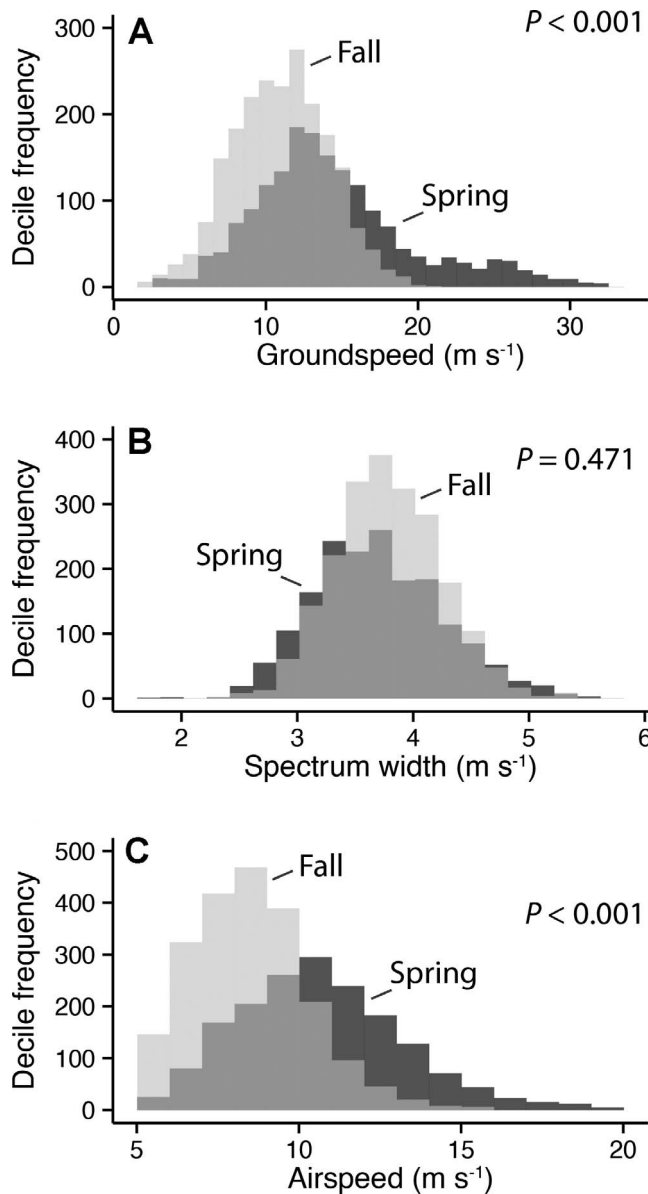


FIGURE 3. (A) Migrant groundspeed, (B) spectrum width, and (C) airspeed distributions during spring (light gray) and fall (dark gray) migratory periods. We excluded airspeeds $< 5.0 \text{ m s}^{-1}$ to reduce effects of insect contamination. See Table 1 for site-specific summaries of the groundspeeds and airspeeds.

$\pm 0.51 \text{ m s}^{-1}$, $P = 0.10$). Groundspeeds changed through the night during spring (LMM; coastal: $-0.05 \pm 0.06 \text{ m s}^{-1}$, $P = 0.121$; inland: $0.32 \pm 0.04 \text{ m s}^{-1}$, $P < 0.001$) and significantly decreased during fall (LMM; coastal: $-0.12 \pm 0.04 \text{ m s}^{-1}$, $P < 0.001$; inland: $-0.12 \pm 0.04 \text{ m s}^{-1}$, $P < 0.001$). We did not find seasonal nor site differences in spectrum width (LMM; $P = 0.471$ and $P = 0.488$, respectively; Figure 3B).

Airspeeds of free-flying migrants, groundspeeds minus the influence of winds aloft, also showed strong seasonal

differences, with spring migrants averaging $2.3 \pm 0.4 \text{ m s}^{-1}$ faster than fall (LMM; $P < 0.001$, Figure 3C). During spring, airspeeds between inland and coastal regions did not differ (LMM; $P < 0.678$), whereas in fall, migrants at inland sites averaged $0.9 \pm 0.3 \text{ m s}^{-1}$ faster (LMM; $P < 0.001$). Airspeeds changed through the night, although generally weakly, during spring (LMM; coastal: $0.06 \pm 0.06 \text{ m s}^{-1}$, $P < 0.05$; inland: $0.13 \pm 0.06 \text{ m s}^{-1}$, $P < 0.001$) and fall (LMM; coastal: $0.09 \pm 0.03 \text{ m s}^{-1}$, $P < 0.001$; inland: $-0.01 \pm 0.03 \text{ m s}^{-1}$, $P = 0.525$).

Although groundspeeds and airspeeds exhibited temporal differences, the marginal variance explained by decile period of the night was less than 3.6%, in comparison to seasonal differences which explained $>25\%$ of the marginal variance.

Flight Strategy

Migrant track direction was to the northeast during spring for inland and coastal regions, whereas heading was comparatively more northerly for coastal sites (Figure 2A, Table 1). During fall, track direction was generally due south and heading due southwest (Figure 2B, Table 1). Overall we found a lower extent of wind drift during spring (slope of $\alpha = 0.39 \pm 0.10$) than in fall (slope of $\alpha = 0.66 \pm 0.12$) (Table 1). Inland sites (spring and fall) and coastal sites (spring) showed little temporal variation in flight strategy over the course of the night (Figure 4A and B). In contrast, fall migrants at coastal sites showed an increased propensity for compensation through the night (Figure 4B). The average PDM during spring for coastal migrants was $38.0 \pm 3.6^\circ$ and $45.2 \pm 3.5^\circ$ for inland migrants (Table 1). During fall PDM was $207.1 \pm 4.3^\circ$ for coastal migrants and $195.7 \pm 4.3^\circ$ for inland migrants (Table 1).

DISCUSSION

Seasonal Differences in Flight Behavior

We observed faster groundspeeds and airspeeds in spring, supporting our hypothesis that migrants fly faster toward rather than away from their breeding grounds. We documented a higher average seasonal airspeed ratio of 1.28 (spring:fall) than those previously reported (1.12–1.19; Karlsson et al. 2012, Nilsson et al. 2013, 2014). By arriving early, migrants are better positioned to have increased access to resources, which can directly influence reproductive fitness (Kokko 1999). Increased airspeeds during spring can also increase flight precision by facilitating greater compensation (Karlsson et al. 2012). Because airspeeds limit migrants' abilities to fully compensate for diverse wind scenarios, subtle changes may lead to substantial differences in migration speeds. For instance, a bird perfectly compensating for a 7.0 m s^{-1} crosswind would see a 14.4% increase in distance covered

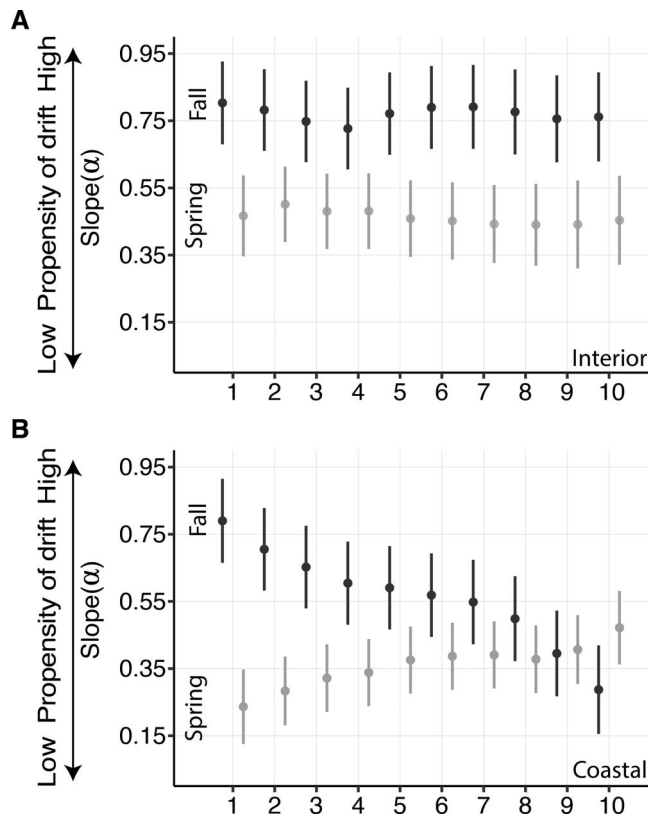


FIGURE 4. (A) Inland and (B) coastal flight strategy during spring (light gray) and fall (dark gray) through the night (decile). Slope of α represents drift propensity; 0: complete wind drift compensation, 1: complete wind drift. Error bars represent 95% confidence intervals. See Table 1 for site-specific summaries of the slope of α .

for a 6-hr flight with a 2.4 m s^{-1} increase in airspeed (spring 10.6 m s^{-1} , fall 8.3 m s^{-1}).

We found an even greater difference in seasonal groundspeeds (spring:fall; 1.39) relative to airspeeds, which were considerably faster during spring (14.7 m s^{-1}) than during fall (10.6 m s^{-1}). Groundspeeds were consistently faster than airspeeds during both seasons: by 4.1 m s^{-1} in spring and 2.3 m s^{-1} in fall. Seasonal wind regimes are partially responsible for groundspeed differences—on average, migrants experienced more tailwinds in spring and more crosswinds in fall—but deciphering ultimate motivations for changes in airspeeds is difficult and potentially complicated by seasonal age and experience differences, resource competition, compensatory ability, and distance from final destination, among other factors. It is also possible that, despite filtering the data, more slow-flying insects were included in the fall samples than the spring samples.

Flight strategies contrasted starkly between seasons, with spring migrants exhibiting greater compensatory tendencies. The difference between mean track and

heading directions across the sites was comparatively lower during spring ($29.6 \pm 1.05^\circ$) than fall ($40.2 \pm 1.06^\circ$), similar to what Bäckman & Alerstam (2003) found. The headings of coastal migrants, both in spring and fall, tended to point inland (Figure 2A and B). Within-night flight strategies were relatively stable, although fall coastal migrants exhibited a more dynamic strategy and compensated more later in the night (Horton et al. 2016). Geography may partly explain these coastal differences, with northbound spring migrants facing much more land to the north than to the east, and fall migrants encountering a tapering coastline heading south. For migrants over coastal areas, the danger of wind drift over the ocean may also account for differences in flight strategies. Surprisingly, fall airspeeds were slower at coastal sites (Table 1), a strategy that hinders the capacity of migrants to compensate for wind drift (Karlsson et al. 2012). One possible explanation for this observation is that slower airspeeds in coastal areas and later in the night reflect differences in the composition of migrants instead of the changing behavior of individuals. Since migrants with lower airspeeds are more prone to coastward drift, these slower-flying birds should be more numerous in coastal areas; this would explain the counterintuitive airspeed result. This also strongly suggests that birds achieve the observed shift toward a compensatory strategy in coastal areas by increasing their track and heading differences (i.e. α), rather than by increasing their airspeeds.

Seasonal differences in flight behavior may also result from the preponderance of young, inexperienced hatch-year individuals during fall, especially in coastal regions (Ralph 1978, Morris et al. 1996, Woodrey and Moore 1997). Although inexperienced migrants do not tend to fly at lower airspeeds (Mitchell et al. 2015), they may be more willing to fly under a greater diversity of wind regimes and may show wider heading distributions (Moore 1984). Age may influence the abilities of migrants to account for wind drift and may explain the occurrence of increased drift during fall (Thorup et al. 2003). Thorup et al. (2003) reported age-dependent wind drift compensation in raptors, with young, first-year individuals showing a greater susceptibility to wind drift. This trend presumably applies to migrant songbirds as well (Ralph 1978), but individual monitoring technology for these assessments in smaller-bodied birds is limited.

Greater dispersion of flight directions could also account for radar-derived airspeed differences across seasons. We predicted this attribute would manifest in seasonally or regionally high measures of spectrum widths (a measure of radial velocity variability). However, this was not evident in our analysis, suggesting that we can attribute airspeed differences to variation in migrant

behavior and not sampling bias due to volume averaging of radial velocities.

Flight Behavior in Response to Changes in Large-Scale Wind Patterns

The observed seasonal, regional, and temporal differences reveal plasticity in birds' flight behaviors. Such plasticity may be important if migrants need to advance their migration phenologies in response to climate change. Decisions made during stopover and in flight influence overall migration speed and may constrain birds' migration strategies without considering additional selection pressures from climate change (Coppack and Both 2002). Tradeoffs between decisions about stopover duration and flight speeds define migration speed, and changing seasonal and regional forces shaping migratory life histories will determine how migrants optimize their behaviors to cope with a changing environment (Alerstam 2011).

Dominant wind patterns may have the greatest effect on migration timing by influencing migrant flight speeds (Kemp et al. 2010, La Sorte et al. 2014). In our study, fall migrants faced substantial crosswinds relative to their PDM (46.2° between PDM and mean wind direction), in contrast to spring (31.3°). Summarizing all nocturnal wind directions (not limited to sampling nights), spring nights exhibited more favorable flying conditions, with winds in the general direction of the PDM $\pm 45^\circ$ on 40.3% of nights; only 22.0% of fall nights showed favorable conditions (chi-square test: $\chi^2 = 77.0$, $P < 0.001$). Thus, during spring birds encountered more tailwinds, and additionally showed more relative compensatory behaviors. This suggests that spring migrants benefitted from more favorable winds, which required lower offsets to compensate for drift when necessary. Furthermore, birds compensated even though displacement would have been less (relative to fall) if they had drifted.

Climate change-induced shifts in wind intensity may influence migration speed, presumably by altering both stopover duration and in-flight migration speed. Wind speeds over the last ~30–60 years have declined across much of North America (Pryor et al. 2009), partly as a result of changes in global climate, and future declines are predicted to be greatest in the eastern United States (~15% decrease in wind speeds; Pryor and Barthelmie 2011). During fall, weaker opposing winds could yield additional nights that are seasonally favorable for migration, thereby reducing stopover duration by providing more opportunities for flight (Erni et al. 2002, Shamoun-Baranes et al. 2006, Kemp et al. 2010, 2013). In flight, declining speeds of seasonally favorable winds would reduce overall ground-speeds and increase energetic expenditure, both during spring and fall. Under these scenarios we predict overall decreases in levels of wind drift, especially during fall. Lower wind speeds would serve to reduce flight speeds and

might reduce seasonal differences in overall phenology. However, because future projections of wind regimes are imperfect, more research is needed to examine the direction and confidence of these changes. Nonetheless, it is clear that these already rapid spring migrations will need to advance further to keep pace with climate change (Coppack and Both 2002). Reduced wind assistance in spring could decrease spatial and temporal flexibility associated with stopover biology.

Additional work is needed to shed light on the motivating factors that drive seasonal flight strategies and the plasticity of these behaviors across greater latitudinal extents. Seasonally appropriate shifts in flight strategy may emerge as migrants approach wintering or breeding grounds (i.e. increased compensation), although no such assessment has been performed to date. Whereas our results demonstrate that migrants are more likely to compensate during spring, we are unable to determine if this pattern varies within the season at more extreme latitudes. Nonetheless, this study demonstrates that weather surveillance radar networks can enable enhanced geographic and temporal coverage to advance our understanding of how migrants moderate migration speeds, cope with wind drift, and alter behaviors across spatial and temporal gradients.

Conclusions

Migrants fly more rapidly and precisely in spring than in fall migration. Although causal processes for these differences may be difficult to define explicitly (i.e. for factors like airspeeds that are under migrants' controls), seasonal changes may indicate a more efficient form of flight during spring or migrants' willingness to engage in more costly (i.e. increased efforts toward precision of flights) behaviors to reach breeding grounds in less time. We found greater wind drift compensation during spring, which may be enhanced by faster airspeeds and increased frequency of favorable wind conditions (i.e. less frequent crosswinds). However, these in-flight factors cannot completely account for seasonal differences in migratory phenology, as stopover duration represents a major component of timing. Regardless, these results are important in understanding migratory behavior in Nearctic–Neotropical migrants; variation in flight behaviors suggests that phenotypic plasticity could be an important factor in migrants' phenological responses to climate change.

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LITERATURE CITED

- Alerstam, T. (1979). Wind as selective agent in bird migration. *Ornis Scandinavica* 10:76–93.
- Alerstam, T. (2011). Optimal bird migration revisited. *Journal of Ornithology* 152:5–23.
- Alerstam, T., and A. Hedenström (1998). The development of bird migration theory. *Journal of Avian Biology* 29:343–369.
- Bäckman, J., and T. Alerstam (2003). Orientation scatter of free-flying nocturnal passerine migrants: Components and causes. *Animal Behaviour* 65:987–996.
- Bates, D., M. Mächler, B. Bolker, and S. Walker (2014). Fitting linear mixed-effects models using lme4. arXiv:1406.5823 [stat].
- Browning, K. A., and R. Wexler (1968). The determination of kinematic properties of a wind field using Doppler radar. *Journal of Applied Meteorology* 7:105–113.
- Buler, J. J., and D. K. Dawson (2014). Radar analysis of fall bird migration stopover sites in the northeastern U.S. *The Condor: Ornithological Applications* 116:357–370.
- Buler, J. J., and R. H. Diehl (2009). Quantifying bird density during migratory stopover using weather surveillance radar. *IEEE Transactions on Geoscience and Remote Sensing* 47:2741–2751.
- Butler, C. J. (2003). The disproportionate effect of global warming on the arrival dates of short-distance migratory birds in North America. *Ibis* 145:484–495.
- Chapman, J. W., R. H. G. Klaassen, V. A. Drake, S. Fossette, G. C. Hays, J. D. Metcalfe, A. M. Reynolds, D. R. Reynolds, and T. Alerstam (2011). Animal orientation strategies for movement in flows. *Current Biology* 21:R861–R870.
- Coppack, T., and C. Both (2002). Predicting life-cycle adaptation of migratory birds to global climate change. *Ardea* 90:369–378.
- Crum, T. D., and R. L. Albery (1993). The WSR-88D and the WSR-88D operational support facility. *Bulletin of the American Meteorological Society* 74:1669–1687.
- Crum, T. D., R. L. Albery, and D. W. Burgess (1993). Recording, archiving, and using WSR-88D data. *Bulletin of the American Meteorological Society* 74:645–653.
- Diehl, R. H., and R. P. Larkin (2005). Introduction to the WSR-88D (NEXRAD) for ornithological research. In *Bird Conservation Implementation and Integration in the Americas: Proceedings of the Third International Partners in Flight Conference* (C. J. Ralph and T. D. Rich, Editors). USDA Forest Service, General Technical Report PSW-GTR-191. pp. 876–888.
- Diehl, R. H., R. P. Larkin, and J. E. Black (2003). Radar observations of bird migration over the Great Lakes. *The Auk* 120:278–290.
- Dokter, A. M., F. Liechti, H. Stark, L. Delobbe, P. Tabary, and I. Holleman (2011). Bird migration flight altitudes studied by a network of operational weather radars. *Journal of The Royal Society Interface* 8:30–43.
- Erni, B., F. Liechti, L. G. Underhill, and B. Bruderer (2002). Wind and rain govern the intensity of nocturnal bird migration in central Europe - A log-linear regression analysis. *Ardea* 90: 155–166.
- Farnsworth, A., B. M. Van Doren, W. M. Hochachka, D. Sheldon, K. Winner, J. Irvine, J. Geevarghese, and S. Kelling (2016). A characterization of autumn nocturnal migration detected by weather surveillance radars in the northeastern USA. *Ecological Applications* 26:752–770.
- Gauthreaux, S. A., and C. G. Belser (1998). Displays of bird movements on the WSR-88D: Patterns and quantification. *Weather and Forecasting* 13:453–464.
- Green, M., and T. Alerstam (2002). The problem of estimating wind drift in migrating birds. *Journal of Theoretical Biology* 218:485–496.
- Horton, K. G., W. G. Shriver, and J. J. Buler (2015). A comparison of traffic estimates of nocturnal flying animals using radar, thermal imaging, and acoustic recording. *Ecological Applications* 25:390–401.
- Horton, K. G., B. M. Van Doren, P. M. Stepanian, W. M. Hochachka, A. Farnsworth, and J. F. Kelly (2016). Nocturnally migrating songbirds drift when they can and compensate when they must. *Scientific Reports* 6:21249. doi:10.1038/srep21249
- Jonzén, N., A. Lindén, T. Ergon, E. Knudsen, J. O. Vik, D. Rubolini, D. Piacentini, C. Brinch, F. Spina, L. Karlsson, M. Stervander, et al. (2006). Rapid advance of spring arrival dates in long-distance migratory birds. *Science* 312:1959–1961.
- Karlsson, H., C. Nilsson, J. Bäckman, and T. Alerstam (2012). Nocturnal passerine migrants fly faster in spring than in autumn: A test of the time minimization hypothesis. *Animal Behaviour* 83:87–93.
- Kemp, M. U., J. Shamoun-Baranes, A. M. Dokter, E. Van Loon, and W. Bouten (2013). The influence of weather on the flight altitude of nocturnal migrants in mid-latitudes. *Ibis* 155:734–749.
- Kemp, M. U., J. Shamoun-Baranes, H. Van Gasteren, W. Bouten, and E. E. Van Loon (2010). Can wind help explain seasonal differences in avian migration speed? *Journal of Avian Biology* 41:672–677.
- Kemp, M. U., J. Shamoun-Baranes, E. E. Van Loon, J. D. McLaren, A. M. Dokter, and W. Bouten (2012). Quantifying flow-assistance and implications for movement research. *Journal of Theoretical Biology* 308:56–67.
- Kokko, H. (1999). Competition for early arrival in migratory birds. *Journal of Animal Ecology* 68:940–950.
- Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen (2014). lmerTest: Tests in Linear Mixed Effects Models. R package version 2.0-20. <https://cran.r-project.org/web/packages/lmerTest/index.html>
- Larkin, R. P. (1991). Flight speeds observed with radar, a correction: Slow “birds” are insects. *Behavioral Ecology and Sociobiology* 29:221–224.
- La Sorte, F. A., D. Fink, W. M. Hochachka, J. P. DeLong, and S. Kelling (2013). Population-level scaling of avian migration speed with body size and migration distance for powered fliers. *Ecology* 94:1839–1847.
- La Sorte, F. A., D. Fink, W. M. Hochachka, A. Farnsworth, A. D. Rodewald, K. V. Rosenberg, B. L. Sullivan, D. W. Winkler, C. Wood, and S. Kelling (2014). The role of atmospheric conditions in the seasonal dynamics of North American migration flyways. *Journal of Biogeography* 41:1685–1696.

- La Sorte, F. A., D. Fink, W. M. Hochachka, and S. Kelling (2016). Convergence of broad-scale migration strategies in terrestrial birds. *Proceedings of the Royal Society of London, Series B* 283:20152588. doi:10.1098/rspb.2015.2588
- Lefcheck, J. S. (2015). piecewiseSEM: Piecewise structural equation modeling in R for ecology, evolution, and systematics. arXiv:1509.01845 [q-bio].
- Mesinger, F., G. DiMego, E. Kalnay, K. Mitchell, P. C. Shafran, W. Ebisuzaki, D. Jović, J. Woollen, E. Rogers, E. H. Berbery, M. B. Ek, et al. (2006). North American regional reanalysis. *Bulletin of the American Meteorological Society* 87:343–360.
- Mitchell, G. W., B. K. Woodworth, P. D. Taylor, and D. R. Norris (2015). Automated telemetry reveals age specific differences in flight duration and speed are driven by wind conditions in a migratory songbird. *Movement Ecology* 3:19. doi:10.1186/s40462-015-0046-5
- Moore, F. R. (1984). Age-dependent variability in the migratory orientation of the Savannah Sparrow *Passerculus sandwichensis*. *The Auk* 101:875–880.
- Morris, S. R., D. W. Holmes, and M. E. Richmond (1996). A ten-year study of the stopover patterns of migratory passerines during fall migration on Appledore Island, Maine. *The Condor* 98:395–409.
- Morris, S. R., M. E. Richmond, and D. W. Holmes (1994). Patterns of stopover by warblers during spring and fall migration on Appledore Island, Maine. *Wilson Bulletin* 106:703–718.
- Newton, I. (2008). *The Migration Ecology of Birds*. Academic Press, London, U.K.
- Nilsson, C., J. Bäckman, and T. Alerstam (2014). Seasonal modulation of flight speed among nocturnal passerine migrants: Differences between short- and long-distance migrants. *Behavioral Ecology and Sociobiology* 68:1799–1807.
- Nilsson, C., R. H. G. Klaassen, and T. Alerstam (2013). Differences in speed and duration of bird migration between spring and autumn. *The American Naturalist* 181:837–845.
- Pryor, S. C., and R. J. Barthelmie (2011). Assessing climate change impacts on the near-term stability of the wind energy resource over the United States. *Proceedings of the National Academy of Sciences USA* 108:8167–8171.
- Pryor, S. C., R. J. Barthelmie, D. T. Young, E. S. Takle, R. W. Arritt, D. Flory, W. J. Gutowski, A. Nunes, and J. Roads (2009). Wind speed trends over the contiguous United States. *Journal of Geophysical Research: Atmospheres* 114:D14105. doi:10.1029/2008JD011416
- Ralph, C. J. (1978). Disorientation and possible fate of young passerine coastal migrants. *Bird Banding* 49:237–247.
- R Core Team (2014). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>
- Shamoun-Baranes, J., E. Van Loon, H. Van Gasteren, J. Van Belle, W. Bouten, and L. Buisson (2006). A comparative analysis of the influence of weather on the flight altitudes of birds. *Bulletin of the American Meteorological Society* 87:47–61.
- Sheldon, D., A. Farnsworth, J. Irvine, B. Van Doren, K. Webb, T. G. Dietterich, and S. Kelling (2013). Approximate Bayesian inference for reconstructing velocities of migrating birds from weather radar. *Association for the Advancement of Artificial Intelligence*:1334–1340.
- Stepanian, P. M., and K. G. Horton (2015). Extracting migrant flight orientation profiles using polarimetric radar. *IEEE Transactions on Geoscience and Remote Sensing* 53:6518–6528.
- Thorup, K., T. Alerstam, M. Hake, and N. Kjellen (2003). Bird orientation: Compensation for wind drift in migrating raptors is age dependent. *Proceedings of the Royal Society of London, Series B* 270:58–11.
- Van Doren, B. M., K. G. Horton, P. M. Stepanian, D. S. Mizrahi, and A. Farnsworth (2016). Wind drift explains the reoriented morning flights of songbirds. *Behavioral Ecology*. doi:10.1093/beheco/arw021
- Van Doren, B. M., D. Sheldon, J. Geevarghese, W. M. Hochachka, and A. Farnsworth (2014). Autumn morning flights of migrant songbirds in the northeastern United States are linked to nocturnal migration and winds aloft. *The Auk: Ornithological Advances* 132:105–118.
- Woodrey, M. S., and F. R. Moore (1997). Age-related differences in the stopover of fall landbird migrants on the coast of Alabama. *The Auk* 114:695–707.
- Zrnic, D. S., and A. Ryzhkov (1998). Observations of insects and birds with a polarimetric radar. *IEEE Transactions on Geoscience and Remote Sensing* 36:661–668.