Title: Migratory flight on the Pacific Flyway: strategies and tendencies of wind drift compensation

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Abstract: Applications of remote sensing data to monitor bird migration usher a new understanding of magnitude and extent of movements across entire flyways. Millions of birds move through the western US, yet this region is understudied as a migratory corridor. Characterizing movements in the Pacific Flyway offers a unique opportunity to study complementary patterns to those recently highlighted in the Atlantic and Central Flyways. We use weather surveillance radar data from spring and fall (1995-2018) to examine migrants' behaviors in relation to winds in the Pacific Flyway. Overall, spring migrants tended to drift on winds, but less so at northern latitudes and farther inland from the Pacific coastline. Relationships between winds and fall flight behaviors were less striking, with no latitudinal or coastal dependencies. Differences in the preferred direction of movement (PDM) and wind direction predicted drift patterns during spring and fall, with increased drift when wind direction and PDM differences were high. Birds also exhibited a looped migration pattern, with more extensive use of the Pacific flyway in spring. Such complex relationships among birds' flight strategies, winds, and seasonality highlight the variation within a migration system. Characterizations at these scales complement our understanding of strategies to clarify aerial animal movements.

1. Introduction

Each spring and fall, billions of migratory birds navigate to and from their breeding and wintering ranges [1–3]. Yet, flight strategies employed during these flights, which can be at high altitudes and often occur at night, are still poorly understood. New technologies are beginning to provide detailed insights into annual activity patterns [4,5], yet still, sampling in-flight behaviors of speed and direction are challenging to acquire, especially of small-bodied birds. These measures are especially important when considering birds' responses to changing atmospheric conditions (e.g., winds aloft). Wind speed and direction are primary drivers for nightly flight initiation [6]; however, en route birds must also contend with being blown off their preferred direction of movement (PDM) by crosswinds [7,8]. To counter the influence of crosswinds, in-flight migrants can compensate by increasing their airspeeds or adjusting their headings (i.e., body axis orientation) to counter wind drift [9]. While heading adjustments minimize overall flight distances, they can lower groundspeeds, thereby slowing the pace of migration and potentially increasing energy expenditure. However, the consequences of drifting off course to unhospitable or deadly environments (e.g., open water) could have ultimate fitness consequences. Season [10,11], topographic barriers [12], and proximity to the breeding destination [13] can shape these flight strategies and fitness consequences.

In North America, the Pacific Flyway – in this case representing bird migration over the land area primarily west of the Rocky Mountains – is generally underrepresented in studies of bird migration, with significantly more research occurring on movements east of the Rockies. This region presents a unique opportunity to test how migrants vary flight strategies in complex and geographically diverse wind patterns [14], varied topography, and season-dependent resource availability [15] across an extensive latitudinal gradient (>15°). To capture the macro-scale orientation strategies of nocturnally migrating birds moving through the Pacific Flyway, we leverage the US weather surveillance radar network [16]. This network allows for a multi-decadal examination of these behaviors, amassing hundreds of thousands of individual measurements of flight activity. These measurements can reveal seasonal timing of migration, the spatial distribution of migrants, and the degree of behavioral plasticity in flight strategies (i.e., the extent to which birds can compensate and drift in changing wind patterns). We hypothesize that the degree of wind drift depends upon proximity to the Pacific coastline, season, and latitude (as an indication of distance to end destination). We predict that migrants drift more further from the Pacific coastline because the risks associated with being blown off course diminishes moving away from open-water [12]. We predict greater levels of drift during the fall because of the abundance of young, inexperienced migrants, and that migrants will drift less as they near their end destinations [13].

2. Material and methods

(a) Weather surveillance radar

We characterized migration intensity, speed, track, and heading across the Pacific Flyway of the United States (Figure 1) by extracting migrant flight data from 19 west coast weather surveillance radar (WSR) stations during spring (March 1st to June 15th) and fall (August 1st to November 15th) from spring 1995 to spring 2018. We acquired radar data through the NEXRAD Level-II archive available publicly on Amazon Web Services (AWS) and processed Level-II data using WSR-LIB [17]. To characterize migratory activity through the night, we subsampled scans every half hour between local sunset and sunrise. We sampled data between 5 km and 37.5 km from the radar in the 0.5-4.5° elevation sweeps and constructed vertical profiles of bird activity from 0-3 km above ground level at 100m intervals [18]. These vertical profiles reflect aggregated nocturnal movements that cannot be attributed to specific species.

We removed precipitation contamination on a per-pixel level within the sampling range using a deep-learning classification algorithm, MISTNET, that leverages a convolutional neural network trained on 239,128 samples, with per-pixel accuracy of 97. 3 % (precision 98.7%; recall 95.9%) [19]. We calculated airspeeds of aerial targets, removing height bins with speeds less than 5 m s^{-1} to exclude insects [20]. We used North American Regional Reanalysis (NARR) [21] data to calculate wind speed and direction within the radar sampling region and linked radar and wind variables to their respective height bins. NARR data are assembled at 3-hour temporal intervals, 32 km spatial resolution, and are modeled at 25 hPa vertical intervals. We calculated airspeed and heading direction using vector subtraction.

(b) Statistics

We estimated the date of peak migration for each WSR station by fitting a generalized additive mixed model (GAMM) to reflectivity with ordinal date as the predictor variable [22]. We included year as a random effect and termed peak migration as the date at maximum predicted reflectivity. To examine the dependence of peak migration date on latitude, we fit a least squares linear model with latitude as the predictor variable. We used two paired t-tests to examine seasonal differences in 1) summed migration activity and 2) slope of α (see below for calculation).

To quantify the degree of wind drift, we used a mixed model approach, regressing track (°) on the difference between track and heading (termed α, °) [23]. This approach generated two metrics describing migrant flight behavior: 1) slope of α, a measure of drift propensity (0, complete wind drift compensation to 1, complete wind drift); and 2) y-intercept, a measure of preferred direction of movement (the composite track direction) under no crosswind drift (PDM) [9]. PDM in our analysis is the aggregate direction of many species (i.e., the nocturnal migration system). We included random intercept terms of station, date, station× date, and station× year [13,24]. We included one random slope term, of α varying on station. We weighted our analysis by the cube root of radar reflectivity. We weighted summaries of migratory track, heading, and measures of drift by the cube root of migratory intensity to prioritize dominant periods of movement [6] and only included data between the α range of -90° to 90° (11.7% of data outside this range).

To summarize the winds migrants used, we weighted wind directions by the product of the cube root of migratory intensity (η) and wind speed (m s^{-1}). Our weighting procedure prioritized winds used by migrants aloft, both by including migrant intensity (i.e., winds used by migrants) and wind speed (i.e., winds with large effect on migrants). This procedure prevented equal weighting of all wind measures.

To examine spatial differences in flight behaviors, we fit a least squares linear model to slope of α with latitude, distance to coastline, and the interaction of latitude and distance to coastline as predictors. Lastly, to determine the dependence of slope of α on differences of PDM and wind direction, we fit a generalized addition model (GAM). These models were fit for each season.

3. Results

We sampled 2,475 nights during spring (458,545 30-min samples) and 2,429 nights (503,735 samples) during fall, totaling 962,280 samples. Spring migration traffic peaked between April 28th and May 17th (May 5th±5.4 days, mean±SD) and fall migration between September 9th and October 7th (September 23rd±6.4 days, mean±SD). Latitude predicted the date of peak migration during spring ($F_{1,17}$=17.79, p<0.001, R^2=0.51) but not during fall ($F_{1,17}$=0.0015, p=0.969, R^2<0.001). Most sites showed higher summed activity in spring compared to fall (13 of 19 sites, Figure 1a, Figure 1c), and the overall mean activity was significantly higher in spring (paired t-test, t_{18}=2.364, p=0.0295).

Spring preferred directions of movement (PDM) ranged between 304.2°(KVTX, see Figure 1a for radar labels) and 23.7°(KPDT) and averaged 347.3°±22.1°(±SD). Fall PDMs ranged between 136.9°(KSOX) and 182.2°(KBHX) and averaged 156.5°±12.6°(±SD) (Figure 1c). The propensity of drift tended to be higher during spring (mean=0.42±0.25, SD) as compared to fall (mean=0.27±0.25, SD); however, this difference was not significant (paired t-test, t_{18}=1.443, p=0.1662, Figure 2a). During spring, latitude and distance to coastline significantly affected propensity of drift (Table S1). Birds generally drifted less with increasing latitude and farther from the coastline (Figure S1). Changes in drift behaviors in relation to distance to coastline were more prominent at southern latitudes (See interaction plot; Figure S1). During fall, we did not find that propensity of drift changed with latitude (p=0.177) or distance to coastline (p=0.453), nor any interaction (p=0.553, Table S1).

Migrants regularly used winds that opposed their seasonal PDMs (Figure 1b, Figure 1d). The absolute value of spring differences between wind direction and PDM decreased with increasing latitude (linear regression, $F_{1,17}$=15.82, slope=-6.759, p=0.0010, R^2=0.482) but did not change with latitude during the fall (linear regression, $F_{1,17}$=0.3767, p=0.547, R^2=0.0217). Differences in PDM and wind direction were predictive of slope of α values, both during the spring (GAM, $F_{2.692}$=8.367, p=0.00107, deviance explained =67.2%, Figure 2b) and the fall (GAM, $F_{2.221}$=3.909, p=0.0283, deviance explained=45.3%, Figure 2c), with greater levels of drift when wind direction and PDM differences were high.

4. Discussion

We quantify for the first time the flight strategies employed by migratory birds passing through the Pacific Flyway. We leverage over two decades of weather surveillance data to characterize migrant track, heading, speed, and density. Migrants varied their aerial behaviors to the complex assemblage of available winds and altered their strategies across gradients of distance to the coastline, season, and latitude.

Geographic and seasonal variation in flight strategies

We observed a general decrease in wind drift with increasing latitudes during spring, supporting the predicted optimal migration strategy of reducing wind drift upon approaching the breeding destination [7,8,13]. Contrary to our prediction, drift decreased farther from the coastline, but only during the spring. However, these behavioral changes also coincided with geographically variable wind patterns. Winds tended to be in greater opposition to northward passage along the southern coastline. It is possible that differences between PDM and wind direction exceed the ability of migrants to compensate and result in elevated levels of drift. These findings contrast behaviors along the Atlantic Flyway, where birds tend to compensate more at coastal sites to avoid being blown over the ocean [12]. Three sites in fall (KHNX, KMUX and KVBX) and one site in spring (KESX) hade α slopes below zero, indicating overcompensation. Overcompensation, could imply correction for previous drift, or topographical effects such as barriers influencing behavior [25].

Looped migratory paths through the western North America

There was 14.5% less migratory activity through the region in fall compared to spring, suggesting that the Pacific flyway is mainly used in Spring. While a decrease in migratory activity is not immediately indicative of a looped pattern of migration, few other scenarios are plausible. Unless fewer birds were leaving their breeding grounds than arriving – a net decrease in population during the breeding season – migrants must be taking an alternative, more easterly route in fall and thereby escaped detection by Pacific flyway radars [15].

Surprisingly, spring wind patterns were in strong opposition to northward passage, particularly in regions with the greatest activity (i.e., Pacific southwest). This finding suggests that other factors are responsible for the shaping of the looped migratory route (e.g., food resources) and not winds aloft, as they are in other looped systems (e.g., Central and Eastern Flyways) [26]. Contrary to other examinations [10,11], wind drift did not vary significantly across seasons, which may reflect first-year migrants using more eastern routes not captured by the 19 Pacific radars. A future investigation examining a larger set of radars, east of the Pacific Flyway, is needed to reveal the interconnectedness of these migratory routes. This result highlights the importance of full annual cycle monitoring and the utility of radar to capture large-scale population dynamics of migratory birds.

5. Conclusion

Flight strategies of migrating birds are fundamental components of their behavioral ecologies and life histories, informed by endogenous (i.e., sensory and physiological) and exogenous (e.g., winds) cues that facilitate navigation and orientation required for their movements in the atmosphere. It is more important than ever to understand and document what shapes these components of migration systems. Human alteration of the planet's surface and atmosphere, whether changing landscapes or loss of habitat, including airspace, is dramatically altering populations of birds and the ecosystems in which they are integral. Remote sensing by radar is critical for studying these patterns, particularly in understudied areas such as the Pacific Flyway. With analyses like this, it will soon be possible to characterize behaviors at the continental scale, linking diverse strategies with complex meteorological and climatological phenomena that can inform new perspectives about the evolution of migration itself.

Ethics. Approval was not required for this study.

Data accessibility. The dataset is provided as electronic supplementary material.

Authors' contributions. PN, CN, AF, and KGH worked to conceive, design, and draft the manuscript. TYL, KW, GB, SM, DS and KGH designed radar algorithms, processed, and summarized radar data. KGH generated figures. All authors provided editorial advice, approved the final version of this manuscript, and are in agreement to be accountable for all aspects of the work.

Competing interests. We declare we have no competing interests.

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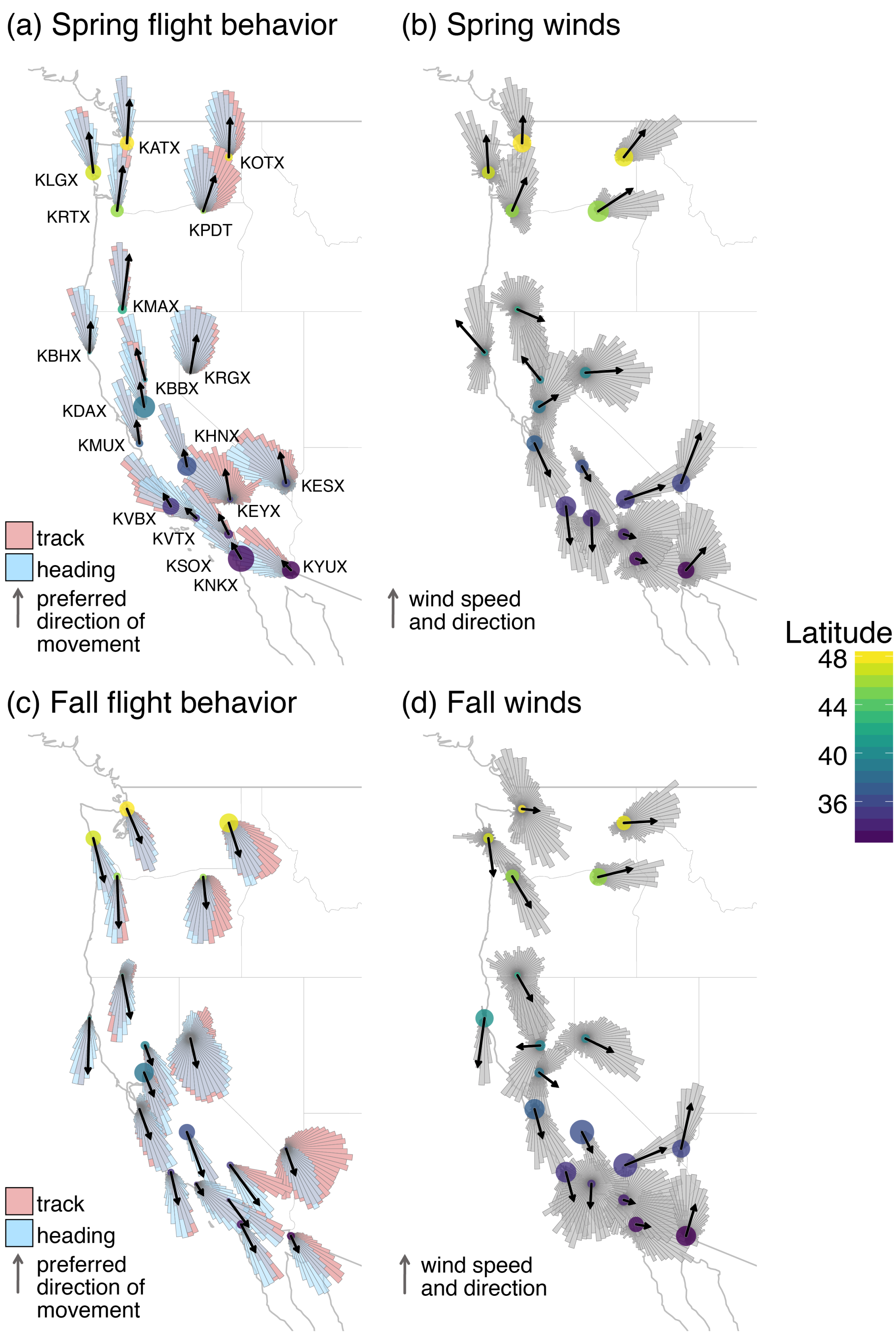

(a) Spring flight behavior
(b) Spring winds
KATX
KLGX
KOTX
KRTX
KPDT
KMAX
KBHX
KRGX
KBBX
KDAX
KHNX
KMUX
KESX
KEYX
KVBX
KVTX
KSOX
KYUX
KNKX
track
heading
preferred direction of movement
wind speed and direction
Latitude
48
44
40
36
(c) Fall flight behavior
(d) Fall winds
track
heading
preferred direction of movement
wind speed and direction

Figure 1: Spring (March 1st to June 15th, a-b) and fall (August 1st to November 15th, c-d) distributions of migrant track (pink), heading (blue), and wind direction (gray) at weather surveillance radar (WSR) stations summarized from 1995 to 2018 between sunset and sunrise. Points show WSR station location and are shaded by station latitude. Station points (a and c) are scaled to the cube-root of the average summed seasonal migration intensity and station points (b and d) are scaled by the rho of wind direction (small points =low directionality). Flight distributions are weighted by the cube-root of flight activity and wind direction by the product of the cube-root of flight activity and wind speed. Arrows' directions denote the preferred direction of movement (a and c) and average wind direction (b and d). PDM arrows' lengths (a and c) are scaled to average migrant groundspeed and wind arrows' lengths (b and d) are scaled to the average wind speed. Note, all distributions are scaled to the same size and number of observations, but exhibit differing maxima. Rose diagrams are summarized in 5° sectors.

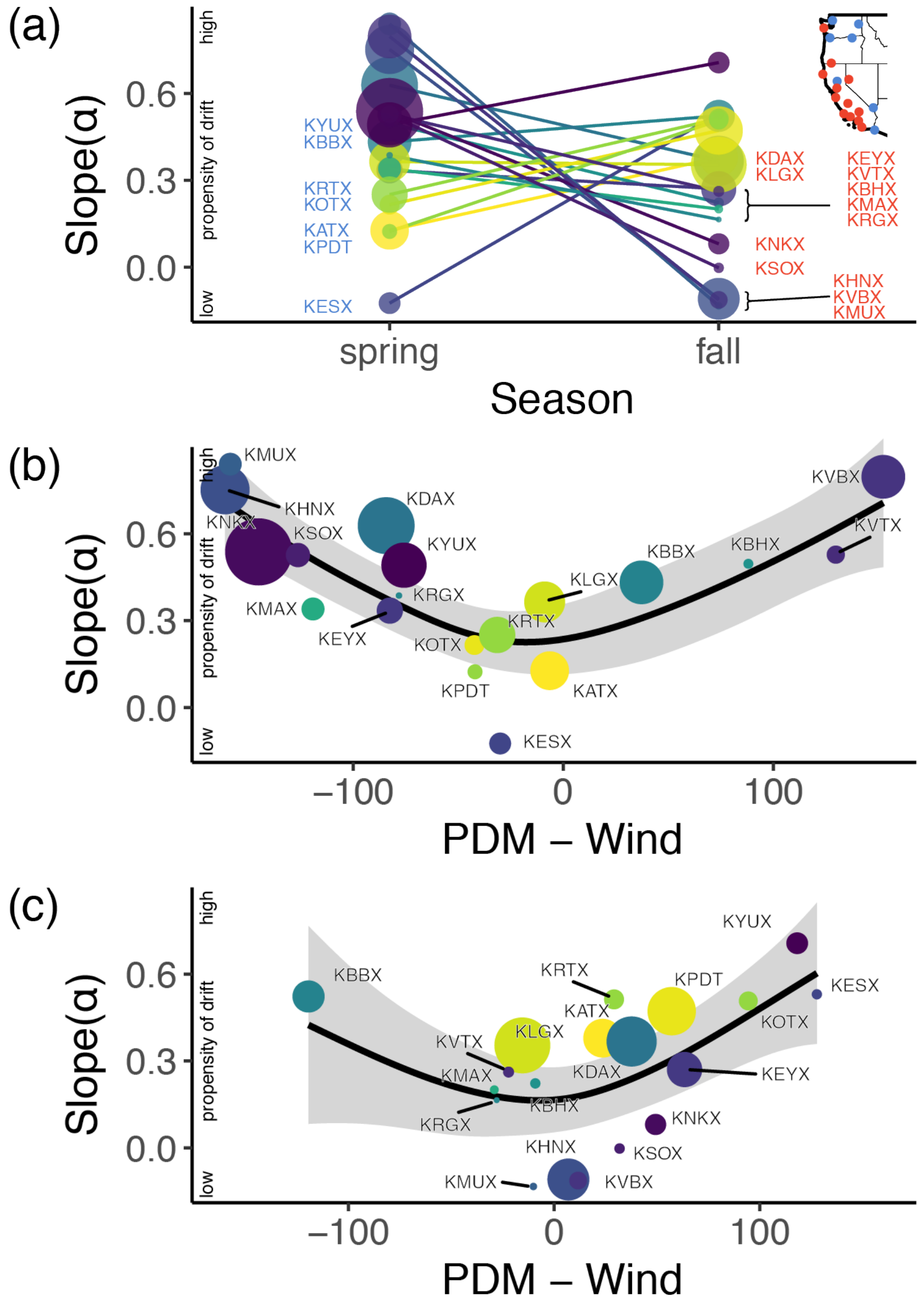

Figure 2: (a) Seasonal propensity of drift (i.e., slope of α). Radar site labels shaded in blue show increasing slope of α values (i.e. more drift) from spring to fall. Those in red show decreasing values (i.e. less drift). Inset shows the locations of decreasing (red) and increasing (blue) drift. (b) Spring and (c) fall mean difference in preferred direction of movement (PDM) and wind direction against the propensity of drift (i.e., slope of α). Gray error bars represent 95% confidence intervals from generalized additive model. All points are shaded by WSR station latitude and the size is scaled to the cube-root of migration intensity.

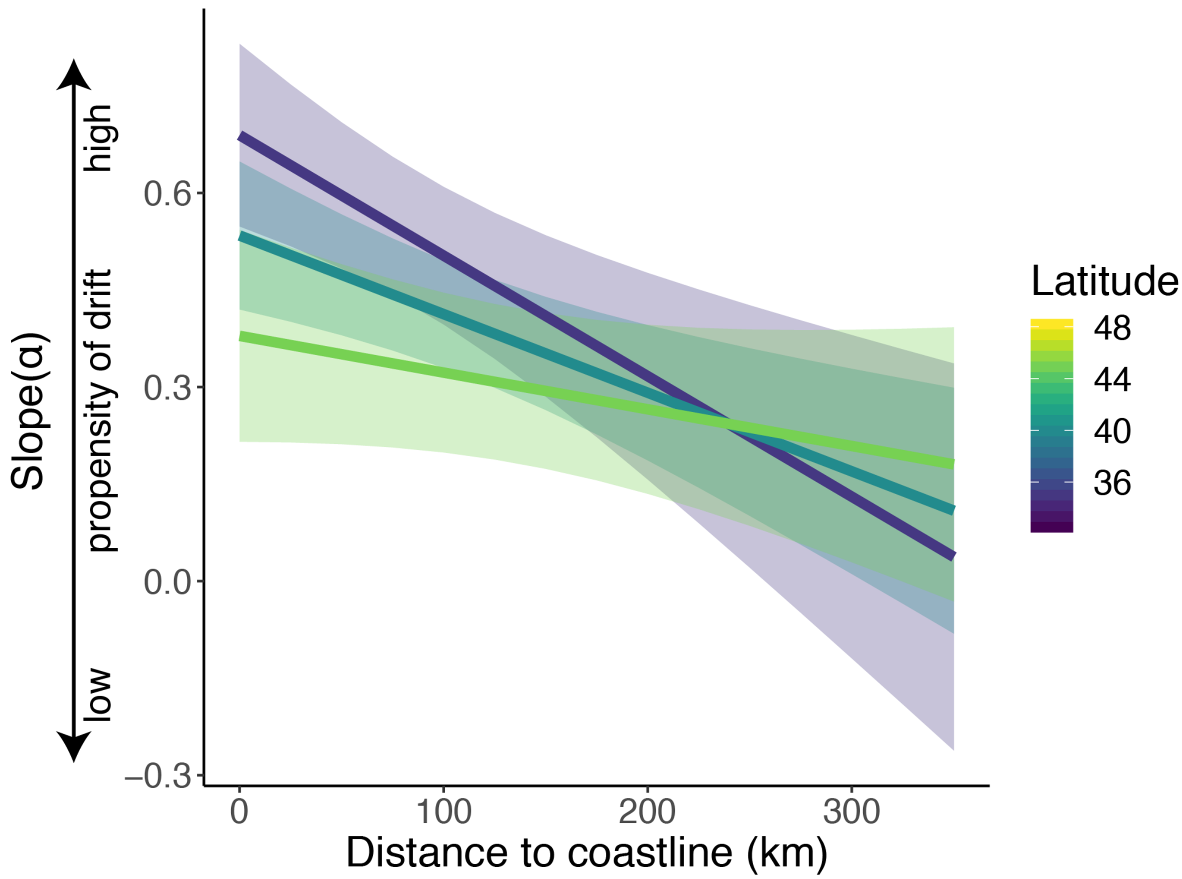

Figure S1: Wind drift propensity across distance to coastline and latitude at 19 weather surveillance radar stations during spring migration (1995-2018). Slope of a represents drift propensity; 0 is complete compensation for wind, 1 is complete drift with wind. Predictions of propensity of drift are shown from 0 to 325 km distance to coastline at 35°N, 40°N, and 45°N. The fitted lines and 95% confidence bands are from a least squares linear model with an interaction between latitude and distance to coastline.

Table S1: Summary of two-way interaction least squares linear model predicting slope of α across 19 weather surveillance stations during spring and fall migratory periods.

Parameter	Estimate	Standard Error	t-value	*P* (>|t|)
Spring				
Intercept	1.775	0.376	4.718	0.000275
Latitude	-0.0310	0.00951	-3.262	0.00525
Distance to coastline (km)	-0.00640	0.00247	-2.594	0.0203
Latitude: Distance to coastline (km)	0.000130	0.0000590	2.199	0.0440
Fall				
Intercept	-0.556	0.537	-1.035	0.317
Latitude	0.0192	0.0136	1.416	0.177
Distance to coastline (km)	0.00271	0.00352	0.771	0.453
Latitude: Distance to coastline (km)	0.0000510	0. 0000840	-0.607	0.553