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Where in the air? Aerial habitat use of nocturnally migrating birds

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The lower atmosphere (i.e. aerosphere) is critical habitat for migrant birds. This habitat is vast and little is known about the spatio-temporal patterns of distribution and abundance of migrants in it. Increased human encroachment into the aerosphere makes understanding where and when migratory birds use this airspace a key to reducing human–wildlife conflicts. We use weather surveillance radar to describe large-scale height distributions of nocturnally migrating birds and interpret these distributions as aggregate habitat selection behaviours of individual birds. As such, we detail wind cues that influence selection of flight heights. Using six radars in the eastern USA during the spring (2013–2015) and autumn (2013 and 2014), we found migrants tended to adjust their heights according to favourable wind profit. We found that migrants' flight altitudes correlated most closely with the altitude of maximum wind profit; however, absolute differences in flight heights and height of maximum wind profit were large. Migrants tended to fly slightly higher at inland sites compared with coastal sites during spring, but not during autumn. Migration activity was greater at coastal sites during autumn, but not during spring. This characterization of bird migration represents a critical advance in our understanding of migrant distributions in flight and a new window into habitat selection behaviours.

1. Introduction

Habitat use is a unifying concept of organismal ecology that connects behavioural plasticity, ecological constraints and evolutionary adaptations of animals to their environment [1]. The lower atmosphere (i.e. aerosphere) is a heterogeneous, dynamic habitat that is occupied by a host of organisms such as birds, bats and insects [2]. Unlike terrestrial habitats, which often can be characterized at smaller scales and in fewer dimensions, biological occupancy of the aerosphere can extend kilometres in altitude above large areas of the Earth's surface. Describing multi-dimensional patterns of use by airborne organisms is essential for characterizing the behavioural processes that drive the distribution and abundance of migrating and foraging animals. Recent technological advances in tracking techniques enable monitoring of long-term airspace use by migratory individuals [3], but the challenges of tracking more than a small number of individuals hampers our inferences about the complete distribution of animals in the aerosphere. Obtaining airspace use distributions, in particular, to resolve details of animals' movements across diverse spatial and temporal scales, poses technical challenges that include processing large amounts of data and exhaustively sampling individuals [4].

Radar remote sensing is one of the few techniques that can accurately quantify multi-dimensional time-series of animal density at high elevations and large

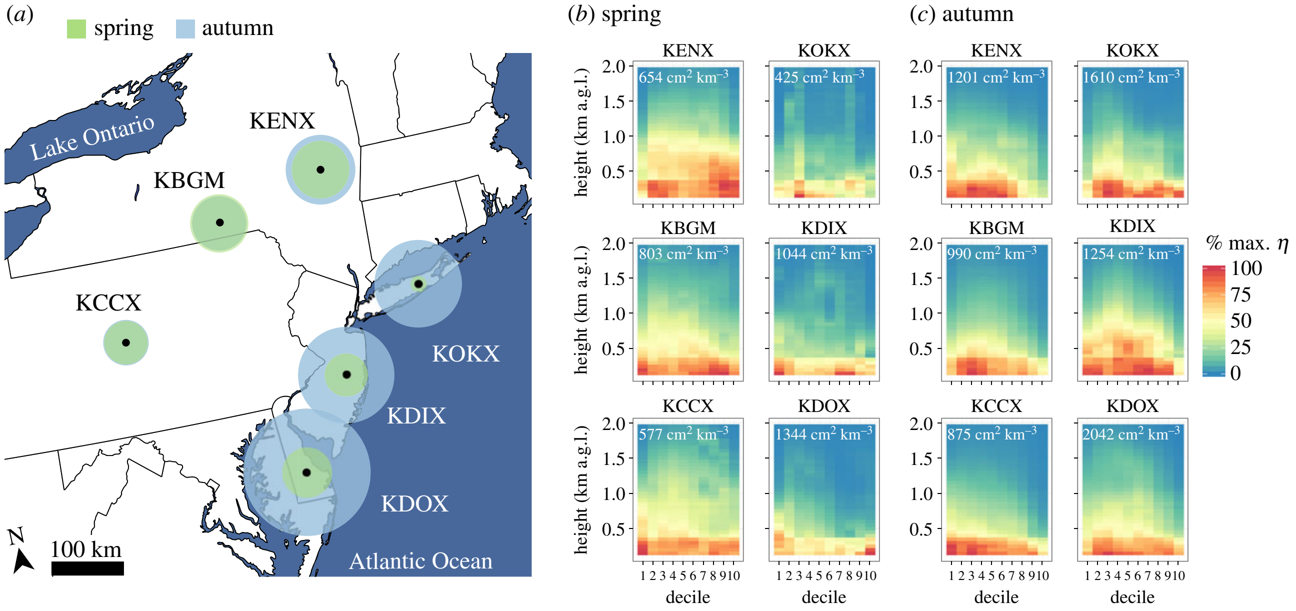

Figure 1. (*a*) WSR-88D locations (black dots). Green (spring) and blue (autumn) disk radius represents the seasonal average of migratory activity (η; cm^2 km^{-3}) as a summation of time and space (i.e. summed η values of *b* and *c*). (*b*) Spring and (*c*) autumn spatial and temporal distribution of η. To use a common gradient of intensity, measures are represented as the percentage maximum for each season–radar pairing. Height intervals were averaged to 50 m intervals to enable visualization.

spatial extents [5]. Radar applications have contributed significant knowledge about biological phenomena, especially bird and insect migration [6,7]. Organized networks of weather surveillance radars such as the United States' NEXRAD or Europe's OPERA can provide continental coverage with multiple updates per hour for monitoring migrant passage and distribution [8,9]. The aim of this paper is to leverage the NEXRAD network to determine where and when nocturnally migrating birds occupy the airspace and how prevailing wind conditions dictate aerosphere use. We build upon previous examinations of height selection and the influence of winds (e.g. [10–12]), examining seasonal and spatial differences in airspace usage. Because wind conditions dramatically influence the efficiency of migratory flight [13], particularly in songbirds, we predict birds will select heights with the greatest wind profit (i.e. support a migrant obtains from wind conditions aloft) to maximize tailwind assistance [10]. In addition, because nights with profitable winds are less frequent during the autumn, we predict correlations with wind profit will be higher during the autumn season [14].

2. Material and methods

(a) Weather surveillance radar

We examined geographical differences in airspace usage following recent evidence from this region of differences in flight strategies between inland and coastal sites [7,14]. We used radar measures from six WSR-88D radars (figure 1*a*): three inland (KENX, KBGM and KCCX) and three coastal (KOKX, KDIX and KDOX). Data were downloaded from NOAA's National Centers for Environmental Information (http://www.ncdc.noaa.gov/has/has.dsselect) from 1 March to 15 June for 2013–2015 and 1 August to 15 November for 2013 and 2014. We generated height profiles of reflectivity factor (Z, mm^6 m^{-3}) at 10 m intervals from 0.15 to 2.0 km above ground level (a.g.l., radar antenna heights; electronic supplementary material, table S1). We used data from the five lowest elevation sweeps (0.5°–4.5°) between a range of 5.0 and 37.5 km from the radar [12]. We converted measures of reflectivity factor to reflectivity (η; cm^2 km^{-3}) following Chilson *et al.* [15]. We manually excluded scans containing non-biological measures (precipitation, anomalous propagation, etc.) through visual inspection and restricted the sampling duration to the hours between evening and morning civil twilight (sun angle 6° below the horizon). We constructed velocity azimuth displays (VADs), retained samples with VAD fits between 1 and 5 root mean square error (RMSE) to limit insect contamination and poor fits, and eliminated samples with airspeeds less than 5.5 m s^{-1} to further reduce insect contamination [16]. We categorized the native 5 and 10 min radar measures between these intervals as tenths of the night (i.e. deciles), averaging measures within these decile periods. We calculated mean flight height by taking the average of the height intervals (10 m) weighted by η.

(b) Winds aloft

To examine wind speed and direction at height intervals occupied by migrants, we used the North American Regional Reanalysis dataset [17]. These data offer a horizontal spatial resolution of approximately 32 km, 3 h updates and 25 hPa pressure-level (i.e. height) intervals of zonal and meridional wind components. We assigned wind measures to decile periods and linked each 10 m height interval of reflectivity to the closest corresponding spatial and temporal measure. We calculated wind profit following [10] using extracted airspeeds from VAD analysis, and used seasonal and site-specific preferred directions of movement extracted from Horton *et al.* [7,14], calculated following [18]. We removed from analysis any sets of conditions in which birds could not fully compensate for cross-winds and for which we could not calculate a real solution [10]. For each height profile, we determined the minimum and maximum wind profit (m s^{-1}), height of the maximum wind profit and the height of the 0.50, 0.60 and 0.75 quantile (τ) of wind profit. To determine the respective height of each quantile, we calculated the median of height bins with wind profits within 0.25 m s^{-1} of the respective quantile value. We calculated the wind profit used by most migrants by taking the mean of wind profits weighted by the vertical profile of reflectivity.

(c) Statistics

We used two-sample *t*-tests to calculate nightly mean height differences across sites (inland versus coastal) and nightly mean

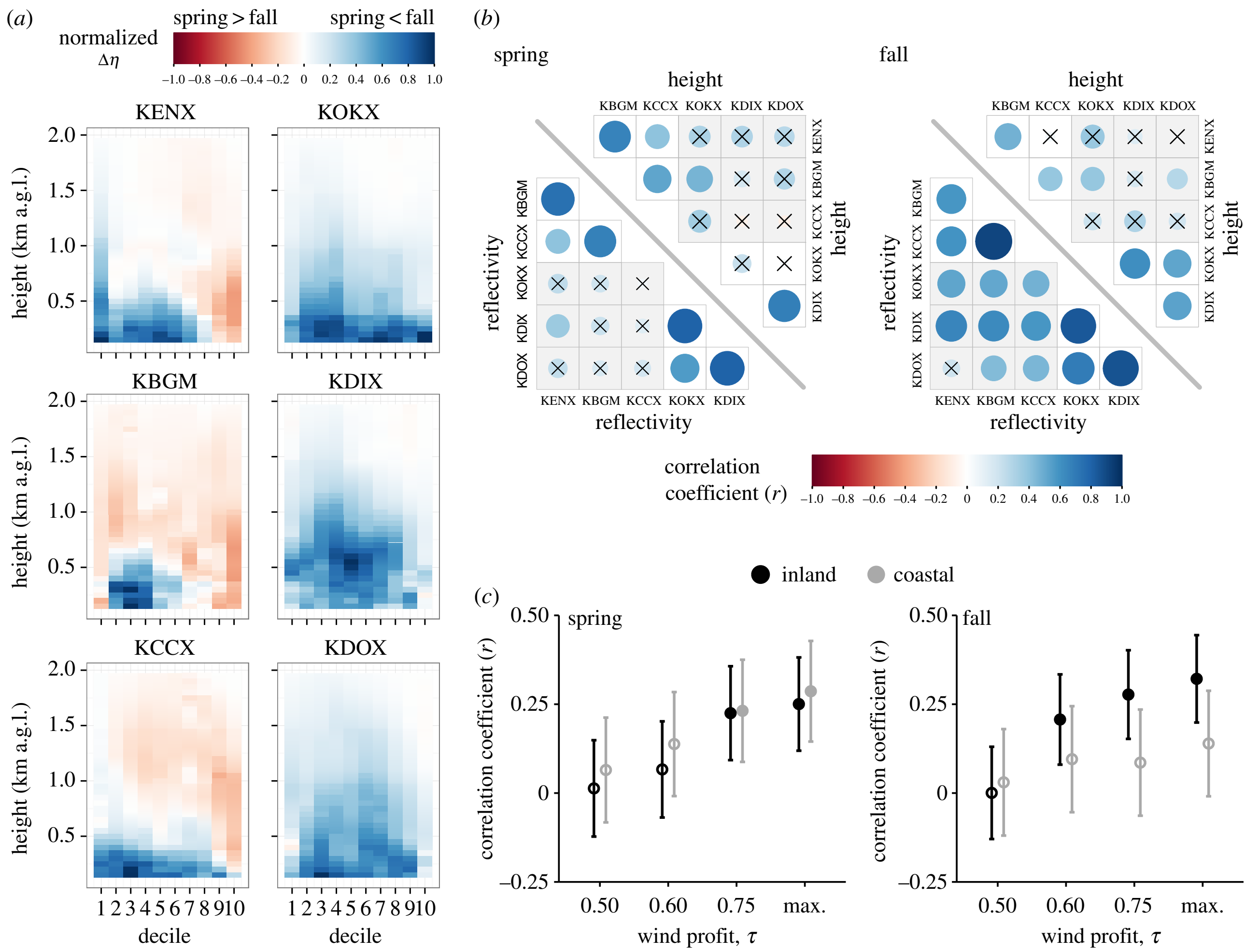

Figure 2. (*a*) Normalized seasonal changes in η. Shades of red represent greater spring migratory activity, whereas blues represent greater autumn migratory activity. (*b*) Seasonal within- (white background) and between- (grey background) region correlations of migrant height and activity. X's denote non-significant Pearson's correlation at the $\alpha = 0.05$ level and circle size is proportional to correlation strength. (*c*) Pearson's correlation ($\pm$95% CIs) between migrant height and height of variable wind profit gain ($\tau = 0.50$, 0.60, 0.75 and maximum wind profit). Statistically significant ($\alpha = 0.05$) Pearson's correlations are denoted by filled points. We used nightly means for all correlations (*b* and *c*).

seasonal differences in maximum wind profit. We used Pearson's correlation to quantify the correspondence of nightly means of migratory activity (reflectivity) and flight height between and within inland and coastal regions (figure 2*b*). We used Pearson's correlations to examine the seasonal and regional relationships between nightly mean flight height and the heights of variable with profit gains ($\tau = 0.50$, 0.60, 0.75 and maximum wind profit).

3. Results

We sampled 136 nights during the spring and 134 nights during the autumn (table 1). We found higher migratory activity (reflectivity) in autumn, particularly over coastal sites (figures 1*a* and 2*a*). Although trends in average reflectivity varied, activity generally peaked in the first half of the night. Average heights of birds in flight ranged from 119.8 to 1135.6 m (table 1), with birds at inland sites flying higher during the spring than birds at coastal sites (inland, 528.8 ± 26.4 m; coastal, 436.0 ± 26.3 m; $t = 4.9$, 407 d.f., $p < 0.01$). During the autumn, regional differences in flight height were less apparent (inland, 435.9 ± 19.7 m; coastal, 451.4 ± 22.8 m; $t = -1.0$, 402 d.f., $p = 0.313$). Birds flew at peak heights during the first 30% of the night and thereafter tended to decrease in height (figure 1*b*,*c*)

Within each region (inland and coastal), migrant activity was positively correlated among radar stations, with six of six possible within-region correlations showing statistical significance during spring and autumn (hereafter represented as spring 6/6, autumn 6/6; figure 2*b*). Correlations between migrant activity at inland and coastal sites were generally weaker or non-significant (spring 1/9, autumn 8/9; figure 2*b*). Correlations between mean nightly flight heights showed similar spatial dependence, with significant positive correlations within regions (spring 4/6, autumn 5/6, figure 2*b*), but weaker non-significant correlations between regions (spring 1/9, autumn 2/9, figure 2*b*).

Maximum wind profits were on average stronger during spring than autumn (spring, 6.9 ± 0.6 m s^{-1}; autumn, 3.3 ± 0.4 m s^{-1}; $t = 10.7$, 790 d.f., $p < 0.001$; electronic supplementary material, figure S1). In spring and autumn, migrants flew at heights positively correlated with the height of the maximum wind profit, and tended to be weaker for heights with moderate wind assistance (figure 2*c*). Regardless, the absolute value differences between the mean flight heights and wind height quantiles were large ($\tau = 0.50$, 500.6 ± 18.3 m; $\tau = 0.60$, 502.6 ± 18.2 m; $\tau = 0.75$, 496.4 ± 23.1 m; $\tau = \text{max.}$, 598.6 ± 34.6 m; mean ± 95% CI; see electronic supplementary material, table S2 for seasonal and regional differences). Birds flew at heights nearer to the maximum wind profit than to the minimum wind profit, suggesting positive selection for wind assistance (spring, $t = -5.0$, 776 d.f., $p < 0.001$; autumn, $t = -8.2$, 804 d.f., $p < 0.001$; electronic supplementary material, figure S2).

Table 1. Weighted means ±95% CI and range of seasonal flight heights (m a.g.l.) for inland and coastal sites.

region	radar	season	sampling nights	flight height (m a.g.l.) ±95% CI	range of flight heights (m a.g.l.)
inland	KBGM	spring	70	484.9 ± 42.5	155.7 – 1127.9
		autumn	96	418.0 ± 26.7	188.4 – 762.2
	KCCX	spring	79	543.0 ± 46.6	199.6 – 1121.1
		autumn	76	424.0 ± 36.3	191.8 – 935.5
	KENX	spring	64	559.1 ± 46.0	213.3 – 1087.6
		autumn	61	479.1 ± 41.6	221.5 – 903.3
coastal	KDIX	spring	72	449.4 ± 45.0	144.8 – 1034.9
		autumn	63	491.2 ± 37.2	253.1 – 870.8
	KDOX	spring	74	438.8 ± 42.0	135.5 – 1048.5
		autumn	83	438.1 ± 38.6	119.8 – 960.7
	KOKX	spring	50	454.6 ± 50.8	172.9 – 1135.6
		autumn	49	419.8 ± 38.1	220.0 – 817.2

4. Discussion

Migrants' flight heights correlated positively with height of the maximum wind profit, although correlations were weaker than expected [10], suggesting more complex relationships between flight height selection. Birds may not select the flight height with optimal wind profit because of time and energy constraints. While higher flight altitudes can extend flight distance because of lower frictional resistance [13], the cost of water loss due to declining partial pressure [19] may result in birds selecting flight altitudes with suboptimal wind profit [10]. Our results suggest that non-aerodynamic constraints, such as costs associated with the time and energy to sample airspace, navigate and stop over [10], may cause migrants to seek conditions sufficient, rather than optimal, for flight.

We found strong seasonal shifts in migration activity in the eastern USA. Significantly greater overall migration activity along more coastal routes typified the autumn season. Coastal sites showed a nearly 100% increase in summed reflectivity (75.5–139.8%) between spring and autumn (figure 1*a*). These patterns may indicate looped migration patterns [20], migrants staging for departure from the coast [21], and possibly population-level drift towards coastal regions [7]. They demonstrate the importance of coastal airspace habitat for autumn migrants, most of which are undertaking their first and most perilous migration. These critical coastal habitats are disproportionately impacted by light pollution and loss of stopover habitat [22].

When examining the spatio-temporal differences in migratory activity (figure 2*a*), we surprisingly saw greater migrant activity during the spring than the autumn at higher altitudes and later in the night. These changes may reflect spring migrants' willingness to fly for longer durations and at higher altitudes to maximize flight distance, a behaviour likely driven by enhanced seasonal tailwind profit.

5. Conclusion

This study is one of the first to present a large-scale, multi-season depiction of the distribution of migratory birds in airspace habitats. We predicted flight altitudes would be strongly constrained by wind speed and direction. Migrants tended to fly at altitudes with high wind profits, but these altitudes were not always the stratum with maximum profit. A more complex scenario likely defines relationships between migrants' flight altitudes, winds, and optimality of movements. Because the altitudinal distribution of wind profit can be very complex, with multiple peaks, in addition to the implicit assumptions of wind profit calculations, we recommend additional analyses across larger scales. Larger-scale analyses will enhance our understanding of how biogeographic effects shape patterns of aerial habitat selection, especially near presumed ecological barriers. By leveraging the existing radar infrastructure, we can examine these patterns through entire migratory flyways and answer macro-scale questions of avian migration.

Data accessibility. The full dataset is available in the electronic supplementary material.

Authors' contributions. All authors worked to conceive and design this study. K.G.H. processed all radar data, generated figures and drafted the manuscript. All the authors have 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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