

Appendix II-F3

Red Knot Satellite Telemetry Study

May 2024

TRACKING OF RED KNOTS ON THE U.S. ATLANTIC COAST: Modeling Movement Patterns and Habitat Use

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Report to:

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List of Acronyms and Abbreviations

AIC- Akaike's Information Criteria

AUC – Area Under the ROC Curve

C – Celsius

Chl *a* – Chlorophyll *a*

CI – Confidence interval

Cm - Centimeter

CTCRW – Continuous-time correlated random walk

h – Hour

HMM – Hidden Markov model

hPa – Hectopascal, 100 pascal

Km – Kilometers

kPa – Kilopascal, 1,000 pascal

m – Meters

m/s – Meters per second

n – Sample size

Pa – Pascal

SD – Standard deviation

SDM – Species distribution model

u – Eastward component of wind

v – Northward component of wind

Δ - Change

1. Executive Summary

Atlantic Shores Offshore Wind LLC (Atlantic Shores) funded a satellite telemetry project tracking Red Knots (*Calidris canutus rufa*) over two migratory seasons in 2020 and 2021 to support further understanding of exposure to (via estimating habitat use and migratory flux) and interaction vulnerability from (via estimating flight height and flight speed) future project development and operations. This report outlines the findings of this project and provides an analysis aimed at improving the understanding of Red Knot habitat use and behavior during staging and migration along the U.S. Atlantic coast using movement and species distribution modeling.

For movement modeling, factors that affect the initiation of migration and migratory strategy (birds that migrate coastally vs. offshore) across multiple years were examined. These results were used to estimate migratory habitat use based on known locations of tracked individuals (realized habitat). Additionally, species distribution modeling was used to estimate available habitat use based on environmental conditions (available habitat).

Together, these results improve consideration of offshore wind development's potential risk to Red Knots. Specifically, this analysis provides information for future risk assessments such as flux rates (i.e., the number of birds passing through an area per unit time) based on habitat use (both realized and available) as well as flight speed and flight height during migratory movements. Furthermore, the results improve understanding of the conditions in which birds initiate migration and the environmental conditions that promote offshore migratory departures.

Movement patterns

During the fall, Red Knots exhibit two distinct movement types — a transit/migratory movement state defined by faster, more directed movements at higher altitudes and a non-migratory/staging movement state defined by slower, less directed movements at lower altitudes. While the factors defining these states were similar between birds of different migration strategies (e.g., birds that migrated coastally vs. those that migrated directly offshore) and years, there were some differences based on environmental conditions:

- Wind speed and direction: Movement patterns were influenced by **wind speed** and **wind direction** for all individuals—birds were more likely to initiate migration with southerly winds, and more likely to continue migrating as wind speed increased. Only Offshore migrants were more likely to initiate migration as wind speed increased, suggesting that utilization of favorable winds for migration may help reduce energy expenditure.
- Pressure and precipitation: Initiation of migration was related to **low pressure**, as Red Knots may take advantage of the onset of active weather like storm fronts. However, this pattern was not robust across years, suggesting flexibility in migratory behaviors or possible variation in pressure or wind conditions across a range of altitudes. Birds were also more likely to switch from migratory to staging as **precipitation** increased, suggesting a balance between using storm fronts to aid migration with contending with post-front rainfall.
- Temperature: The relationship with **temperature** varied between migrant type (coastal vs. offshore migrants) and year, suggesting its importance is contextual. While all individuals were more likely to initiate migratory as temperature increased, offshore migrants remained migrating

during warmer temperatures, but only in 2021, so this relationship could be more complex or due to sampling variation between years.

Habitat use

- Coastal vs. offshore: Kernel density estimates showed high densities in coastal areas for both non-migrating/staging and migratory movement of coastal individuals, contrasting greater use of pelagic habitats for offshore migrants. The results can inform potential exposure to offshore wind development, including the Atlantic Shores lease area, but is limited to habitat that tracked individuals used and represents a coarse estimate of density.
- Potential offshore pathways: Combining all data, **coastal habitats were areas of highest potential use, with overwater activity decreasing with distance to shore**. The species distribution modeling approach identifies potential overwater habitats; together with kernel density, these estimates inform our understanding of potential exposure to offshore wind energy development.
- Factors influencing distribution: Species distribution modeling revealed patterns of potential available habitat, with **latitude** and **distance to shore** as important variables contributing to probability of occurrence for Red Knots. These variables can be used to understand the potential factors influencing offshore habitat use on a broad spatial scale.

2. Introduction

This research aims to improve understanding of the migratory habitat use and behavior of Red Knots during staging and migration along the U.S. Atlantic coast. Specifically, to improve understanding of the potential risks imposed on the species from offshore wind development, in association with two Atlantic Shores Lease Areas OCS-A 0549 and OCS-A 0499. Offshore movements are of particular concern to proposed wind developments; determining the conditions when animals move offshore and what habitats they use is critical to understanding exposure risk. This study utilized tracking data collected in 2020 and 2021 coupled with movement modeling (hidden Markov modeling; HMM) and species distribution modeling (SDM) strategies to better understand habitat use and movements of Red Knots during migration. The tracking effort used in this analysis is detailed in a report submitted to the Bureau of Ocean Energy Management (BOEM) by Atlantic Shores on April 14, 2022 titled "*Tracking Movements of Red Knots in the U.S. Atlantic Using Satellite Telemetry, 2020-2021*" (Feigin et al. 2022).

Objectives for movement modeling include: (1) developing a model to distinguish between staging/non-migratory and migratory movements based on the distance between subsequent locations (i.e., step length or velocity), turning angle, and altitude; (2) examining how weather, timing, and intrinsic factors relate to birds transitioning between movement modes; (3) exploring whether there are distinctions between the influence of environmental conditions in the movement patterns of sub-populations that use coastal and offshore migration routes; and (4) exploring the level of interannual variation in these effects. With SDMs, the objectives include: (1) determining what offshore flyways; and (2) examining how these factors combine to define the species offshore habitat use and range. This analysis provides information associated with the potential risk imposed by future offshore wind projects to Red Knots through improved estimation of habitat use (both realized and available), flight speed as it relates to potential flux across lease areas, and flight height specific to migratory movement.

3. Methods

3.1. Capture and Tagging

All field work to capture and tag Red Knots was conducted under the direction of Dr. Larry Niles of WRP (Feigin et al. 2022). Captures occurred at Brigantine Natural Area (39°26'35"N, 74°19'45"W) in coastal New Jersey in 2020 (August 13, 22, 24; n=29) and 2021 (August 21, 23, 24, 26, n=31), timed to maximize the number of transmitters deployed on long-distance Red Knots likely to depart from the Atlantic coast by mid-September. Red Knots were captured using cannon nets following established protocols and were banded with one standard USFWS metal band and a light-green leg flag with a field-readable black alpha-numeric code. Mass was collected and age class was determined (if possible) by plumage characteristics and molt condition. PinPoint Argos-75 GPS transmitters (Lotek Wireless, Ontario, Canada) were attached to Red Knots by clipping a small area of feathers from synsacral region and gluing tags to the feather stubble and skin with a cyanoacrylate gel adhesive. Two subcutaneous sutures were inserted at the distal and proximal ends of the tags to improve transmitter retention. This glue-and-suture method has been used to attach transmitters to Common and Roseate terns in the eastern U.S. with no evidence of adverse effects (Loring et al. 2016, Loring et al. 2019). Each transmitter weighed (4.1 g), <3% of the average body mass of tagged Red Knots (average 171 g), and each had a 5 cm GPS antenna and 3 cm Argos antenna. These transmitters were designed to collect 60 GPS locations, and altitude estimates with 2020 tags were programmed to collect five locations per day for 12 days, while 2021 tags were programmed to collect

hourly locations. Location data was relayed online via the Argos satellite system (<https://www.argos-system.org/>).

3.2. Data Management and Analysis

All data management and analysis were conducted in R version 4.1.0 (R Core Team 2023) and ArcMap version 10.8.1 (ESRI, Inc., Redlands, CA, USA). Of the 29 tags deployed in 2020, 18 tags failed to record data, with an additional tag excluded due to suspected tag failure or loss. Of the 31 tags deployed in 2021, two failed to record data, with additional six individuals excluded due to suspected tag failure or loss, or where fewer than 10 data points were collected. Erroneous outlying points, those determined to be far beyond realistic daily migratory movements based on distance between subsequent locations for particular individuals, were removed manually prior to analysis.

Red Knots exhibit two distinct migratory strategies: (1) “offshore” or “long-distance migration,” whereby individuals head directly offshore from staging areas in New Jersey and migrate to South America, and (2) “coastal” or “short-distance migration,” whereby individuals move down the coast to multiple staging areas before making a shorter offshore movement down to Cuba and other nearby islands and South America, generally departing from North or South Carolina. To explore the potential differences in covariates relating to transitions between staging and migratory movement for these groups, a categorical variable for these two groups was created (defined based on observed migratory track) to explore potential interactions with covariates. Five individuals were excluded from movement modeling that only had location data at the initial staging site, and migrant type could not be determined. In addition, given that all but one individual from 2020 was categorized as the “offshore” migrant type, the focus of the interannual comparison was on “offshore” individuals, and the one “coastal” individual was excluded from the movement analysis. As a result, GPS data from nine individuals from 2020 and 18 individuals from 2021 were included in the HMM movement analyses. Ten individuals from 2020 and 24 individuals from 2021 were included in SDMs (Table 1).

Satellite-derived environmental covariates were chosen based on *a priori* knowledge of shorebird habitat use and movement (Loring et al. 2020b, 2020a) and included wind speed and direction (here defined as the magnitude and direction of the wind vector), temperature, precipitation, and air pressure. At-height weather data were available at 37 pressure levels (1–1000 hPa) for which geopotential height was also available. For individual locations at an estimated altitude at or below 10 m, the surface-level dataset was used to extract wind, pressure, and temperature information based on the closest 1 h interval to the timestamp of the tracking data. For individual locations at estimated altitudes greater than 10 m, wind vector, pressure, and temperature data were vertically interpolated to estimated flight altitudes using linear interpolation between the closest altitude fields based on geopotential height (which varies within pressure levels based on environmental conditions). Ground speed (m/s) was calculated based on Red Knot tracking data locations and times, and used in combination with wind u and v vectors at altitude to calculate wind support (defined as the amount of tailwind in relation to the speed and direction of movement; (Shamoun-Baranes et al. 2007). Euclidean distance was used to calculate distance to shore.

In addition to the above environmental covariates, the potential influence of weight at capture, date, and time of day (day vs. night) on movement behavior was also examined. Prior to inclusion in the HMMs, all covariate data were scaled and zero-centered. Log transformations were applied for covariates with high degrees of skew. Correlation among variables was examined to determine the final covariates included in

models, and all covariates had Pearson’s correlation <0.5. Wind speed and direction were strongly correlated and related to wind support, and as such, we compared models with wind direction and wind speed with those with wind support. Sex classification was not available, and all but one individual were determined to be after second year (ASY), as such, age and sex were not included in the analysis.

Table 1. Red Knot individuals included in the analysis and corresponding year, capture weight (g), migrant type classification (offshore, coastal, unknown), and which models the data was included in: Species Distribution Model (SDM) or both (SDM and hidden Markov models).

Individual ID	Year	Capture Weight	Migrant Type	Models
204351	2020	199	Offshore	Both
204352	2020	211	Offshore	Both
204357	2020	182	Offshore	Both
204359	2020	166	Offshore	Both
204361	2020	186	Coastal	SDM
204364	2020	164	Offshore	Both
204369	2020	161	Offshore	Both
204370	2020	190	Offshore	Both
204371	2020	179	Offshore	Both
204375	2020	175	Offshore	Both
224073	2021	192	Offshore	Both
224075	2021	153	Offshore	Both
224076	2021	166	Unknown	SDM
224077	2021	183	Coastal	Both
224078	2021	170	Coastal	Both
224079	2021	180	Unknown	SDM
224080	2021	189	Coastal	Both
224081	2021	161	Coastal	Both
224082	2021	163	Coastal	Both
224083	2021	191	Offshore	Both
224085	2021	174	Coastal	Both
224087	2021	151	Unknown	SDM
224088	2021	152	Offshore	Both
224089	2021	160	Offshore	Both
224091	2021	138	Unknown	SDM
224092	2021	163	Coastal	Both
224093	2021	189	Offshore	Both
224095	2021	202	Coastal	Both
224096	2021	169	Unknown	SDM
224097	2021	175	Offshore	Both
224098	2021	192	Unknown	SDM
224099	2021	201	Offshore	Both
224102	2021	180	Coastal	Both
224103	2021	192	Coastal	Both

Table 2. Environmental covariate datasets used in the Red Knot species distribution models (SDM) and hidden Markov modeling (HMM) including the spatial resolution (spatial), temporal resolution (temp.), heights at which data were available (height; “at height” refers to data available at 37 pressure levels ranging from 1–1000 hPa), and the source of the dataset.

Covariate	Temp.	Spatial	Height	Analysis	Data Source
Wind speed (m/s)	0.25°	Hourly	10m, at height	SDM, HMM	Derived from <i>u</i> and <i>v</i> wind vector data. ERA5 reanalysis for global climate and weather dataset ^{1,2}
Wind direction (degrees)	0.25°	Hourly	10m, at height	SDM, HMM	Derived from <i>u</i> and <i>v</i> wind vector data. ERA5 reanalysis for global climate and weather dataset ^{1,2}
Wind support	0.25°	Hourly	10m, at height	HMM	Derived from <i>u</i> and <i>v</i> wind vector data, and speed and angle of movement of individuals. ERA5 reanalysis for global climate and weather dataset ^{1,2}
Temperature (°C)	0.25°	Hourly	2 m, at height	SDM, HMM	ERA5 reanalysis for global climate and weather dataset ^{1,2}
Pressure (Pa)	0.25°	Hourly	10 m, at height	SDM, HMM	ERA5 reanalysis for global climate and weather dataset ^{1,2}
Precipitation (m)	0.25°	Hourly	Surface	SDM, HMM	ERA5 reanalysis for global climate and weather dataset ¹
Distance to shore	1 km	Static	Surface	SDM	Derived from Global Self-consistent, Hierarchical, High-resolution Geography Database amalgamated from World Vector Shorelines and CIA World Data Bank II ⁵

¹ERA5 hourly data on single levels from 1979 to present, Copernicus Climate Change Service (C3S) Climate Data Store (CDS) H. Hersbach, B. Bell, P. Berrisford, G. Biavati, A. Horányi, J. Muñoz Sabater, J. Nicolas, C. Peubey, R. Radu, I. Rozum, D. Schepers, A. Simmons, C. Soci, D. Dee, and J.-N. Thépaut. <https://doi.org/10.24381/cds.adbb2d47>

²ERA5 hourly data on pressure levels from 1979 to present, Copernicus Climate Change Service (C3S) Climate Data Store (CDS). H. Hersbach, B. Bell, P. Berrisford, G. Biavati, A. Horányi, J. Muñoz Sabater, J. Nicolas, C. Peubey, R. Radu, I. Rozum, D. Schepers, A. Simmons, C. Soci, D. Dee, and J.-N. Thépaut. <https://doi.org/10.24381/cds.bd0915c6>³ General Bathymetric Chart of the oceans GEBCO 2021 Grid.

https://www.gebco.net/data_and_products/gridded_bathymetry_data/

⁴ Copernicus Land cover classification grid. <https://cds.climate.copernicus.eu/cdsapp#!/dataset/satellite-land-cover?tab=overview>

⁵ Global Self-consistent, Hierarchical, High-resolution Geography Database. <https://www.ngdc.noaa.gov/mgg/shorelines/>

⁶ Copernicus Marine Environment Monitoring Service interpolated GlobColour. <https://doi.org/10.48670/moi-00100>

3.3. Hidden Markov Models

HMMs provide a powerful tool to examine underlying behavior states based on movement trajectories. These models are specified with an observation time series and an underlying non-observable (hidden) state sequence (Patterson et al. 2008, Langrock et al. 2012). The observable variables relate to movement data, composed of two data streams, step length and turning angle, calculated for each of the t time steps of observed position based on latitude and longitude. Step length is calculated as the Euclidean distance between locations at time $_t$ and time $_{t+1}$, while turning angle is calculated as the change in bearing between the intervals $[t-1, t]$ and $[t, t+1]$ (McClintock and Michelot 2018). Additional data streams (e.g., flight height) can be incorporated into models to aid in distinguishing behavior states. An individual may switch among a set of discrete movement states that are characterized by distributions for the included data streams, and the unobserved state sequence is assumed to be a Markov chain. In the context of animal movement, the hidden states in HMMs can be interpreted as proxies for behavior states, in this case distinguishing between non-migratory/staging and migratory movement. These models can then examine the degree to which different environmental or intrinsic factors influence transitions between

movement states. HMMs were implemented in the *momentuHMM* R package (McClintock and Michelot 2018).

Discrete-time HMMs assume equal time steps between sequential locations. Given differences in data collection intervals for 2020 and 2021 data, as well as missing altitude information for 2020 (39% of locations missing altitude), a two-pronged approach was taken for this analysis. First, the 2021 data was analyzed for which the equal time step assumption was met (6 h time interval), and there was no missing altitude information in the HMM framework described above using step length, turning angle, and altitude as data streams to examine the influence of environmental covariates on transitions between staging and migratory states and differences between migrant types. Second, to examine the level of interannual variation in these relationships, data were combined across years and used a continuous-time correlated random walk (CTCRW) model using the *crawl* R package (Johnson et al. 2008) to predict locations at 6-hour time interval (to meet the assumption of equal time steps between sequent locations in discrete-time HMMs). Analysis of “offshore” migrants from both years ($n=17$) was conducted using only step length and turning angle as data streams and surface-level environmental covariates (given missing altitude information). “Coastal” migrants were excluded as there was only one individual in 2020 in this category.

3.3.1. 2021 HMM

States were chosen based on *a priori* understanding of behavior and included migratory behavior, represented by a state with strong directionality (i.e., high angle concentration), larger step lengths, and higher altitudes, and non-migratory/staging represented by shorter step lengths, greater turning angles (i.e., low angle concentration), and lower altitudes. While a three-state model to split the staging state into area-restricted and coastal movement states was explored, the model could not distinguish a third state given the data. Turning angle was assumed to have a wrapped Cauchy distribution, a circular distribution (McClintock and Michelot 2018), and step length and altitude a gamma distribution. Step length and altitude mean and standard deviation along with angle mean and concentration were estimated for each state. Verification that models identified global maxima by refitting the null model with randomized initial parameter values ($n=1,000$) was completed and used parameter starting values for the best fit iteration (based on Akaike’s Information Criteria) for subsequent models. To examine the overall importance of different covariates on the movement states of Red Knots, as well as potential differences between migrant types (e.g., offshore, coastal), two global models were run with and without interactions with migrant type that included wind speed, wind direction (cosinor circular covariate), temperature, pressure, precipitation, date (ordinal), time of day (day/night), and capture mass. Wind speed, wind direction, temperature, and pressure values were those at altitude. We also explored substituting wind support for wind speed and direction, but found lower support for those models based on AIC (Table 3). Given this comparison and interest in overall patterns, as well as the differences between the two migrant types, the results of both models (with wind speed and direction) are presented (Table 4). The Viterbi algorithm was used to compute the most likely sequence of states, assigning a state to each location in the time series using the most complex model (McClintock and Michelot 2018). To compare space use across migration strategies and for comparison with species distribution modeling results (see below), locations assigned to the migratory state for 2021 data were used to calculate non-parametric fixed kernel densities by migrant type (coastal, offshore). Smoothing factors were chosen based on reference bandwidth calculation.

3.3.2. 2020-2021 HMM

Interannual models were run similarly to the above method with the exclusion of altitude as a data stream. To examine the potential interannual differences, two global models were run with and without interactions with year that included (surface level) wind speed, wind direction (cosinor circular covariate), temperature, pressure, precipitation, date (ordinal), time of day (day/night), and capture weight. As above, the results are presented from both models (Table 5).

3.4. Species Distribution Modeling

To assess offshore habitat use of Red Knots during fall migration, GPS tag fixes from 34 individuals were compared to pseudo-absence locations generated within the area covered during their fall migration (extent: latitude [-84, -39], longitude [-1, 51]). Both known locations (951 locations) and pseudo-absences (8761 locations) were filtered to only include points over water (depth > 2m), as the focus of this analysis is solely on offshore habitat use. There are a variety of ways to create pseudo-absences when using telemetry data to build species distribution models, many of which can bias the results of the analysis (Hazen et al. 2021). While using movement models to create plausible pseudo-absences is effective in some cases, in this study the technique was found to bias results away from the starting or ending points of the tracks (i.e., the coasts of North and South America). As such, we used a randomized draw of points in the study area (the bounding box of all observed locations of the animals). This approach incorporated five times the number of pseudo absences than observations to create effective models that removed the above-described bias and created a more balanced assessment of fall staging and migratory space use.

After all observations and pseudo-absences were compiled, environmental covariate values were assigned to each. As there is no altitude information associated with the pseudoabsences, observation-specific information could not be used to associate the data with environmental covariates at altitude (Table 1). Rather, for all data points, environmental covariates (Table 2) from 4 different standardized altitudes were associated at four altitudes: surface (2–10 m), 50 m, 300 m, 1,000 m above sea level). Environmental covariates represented fall (August - September) averages by year (2020 and 2021) and were associated with all points to describe a broader static distribution with environmental averages and climatologies rather than hourly changes in behavior or habitat use used in the movement modeling.

Once complete, the observations, pseudo-absences, and associated covariates, were incorporated into a boosted regression tree machine learning framework using the *dismo* package (Hijmans et al. 2021). These models are effective at making predictions as they can manage many correlated predictor variables and handle complex relationships between covariates and the response variable. Due to issues with algorithm convergence among weather variables, only surface level weather was incorporated in the model. A model was fit using latitude, distance to shore, and all the surface level weather climatologies with a learning rate of 0.02, a bag fraction of 0.75, and no interactions among predictors (tree complexity of 1).

Cross-validation was used to assess model fit and adds 50 trees at each pass until the residual deviance on holdout data is minimized, yielding the optimal number of trees in the final model. The Area Under the ROC Curve (AUC) metric (a test to determine the accuracy of binary predictions) was used to assess model fit and tested for improvements. AUC was estimated using a cross-validation protocol using 10 folds.

3.4.1. SDM Predictions

The best fit model was used to predict the distribution of Red Knots during the fall migration season across years, with predictions representing the expected probability of occurrence (ranges from 0 to 1). The study area was divided into a 10 x 10 km grid, and all environmental covariates were associated with the centroid of each cell. August and September averages for all covariates were used to make one overall habitat use prediction. For improved visualization, the final predictions were upscaled to 20 km grid resolution.

4. Results

4.1. Movement Modeling

Red Knots during fall migration in 2020–2021 experienced a range of environmental conditions (Figure 1). The 2021 HMMs revealed two distinct movement states that matched the hypothesized staging and migratory states (Figure 2; Figure 3). The staging state represented shorter distance and less directional movement at lower altitude, with a mean step length of 3.21 ± 4.02 km (SD), mean altitude of 9.27 ± 8.21 m and angle mean \pm concentration of -3.12 ± 0.51 radians, while the migratory state represented longer more directed movement at greater altitude, with a mean step length of 215.63 ± 172.14 km, mean altitude of 285.05 ± 511.35 m and angle mean \pm concentration of -0.06 ± 0.78 . The percentage of time spent in the staging state was higher than the migratory state for both offshore (79%) and coastal (85%) migrants. The interannual HMMs revealed similar step and angle parameters to the 2021 HMM. The staging state had a mean step length of 4.06 ± 4.90 km and angle mean \pm concentration of -3.08 ± 0.20 , while the migratory state had a mean step length of 226.87 ± 117.72 km and angle mean \pm concentration of -0.02 ± 0.88 . The percentage of time individuals spent in the staging state was higher than the migratory state in both 2020 (67%) and 2021 (78%).

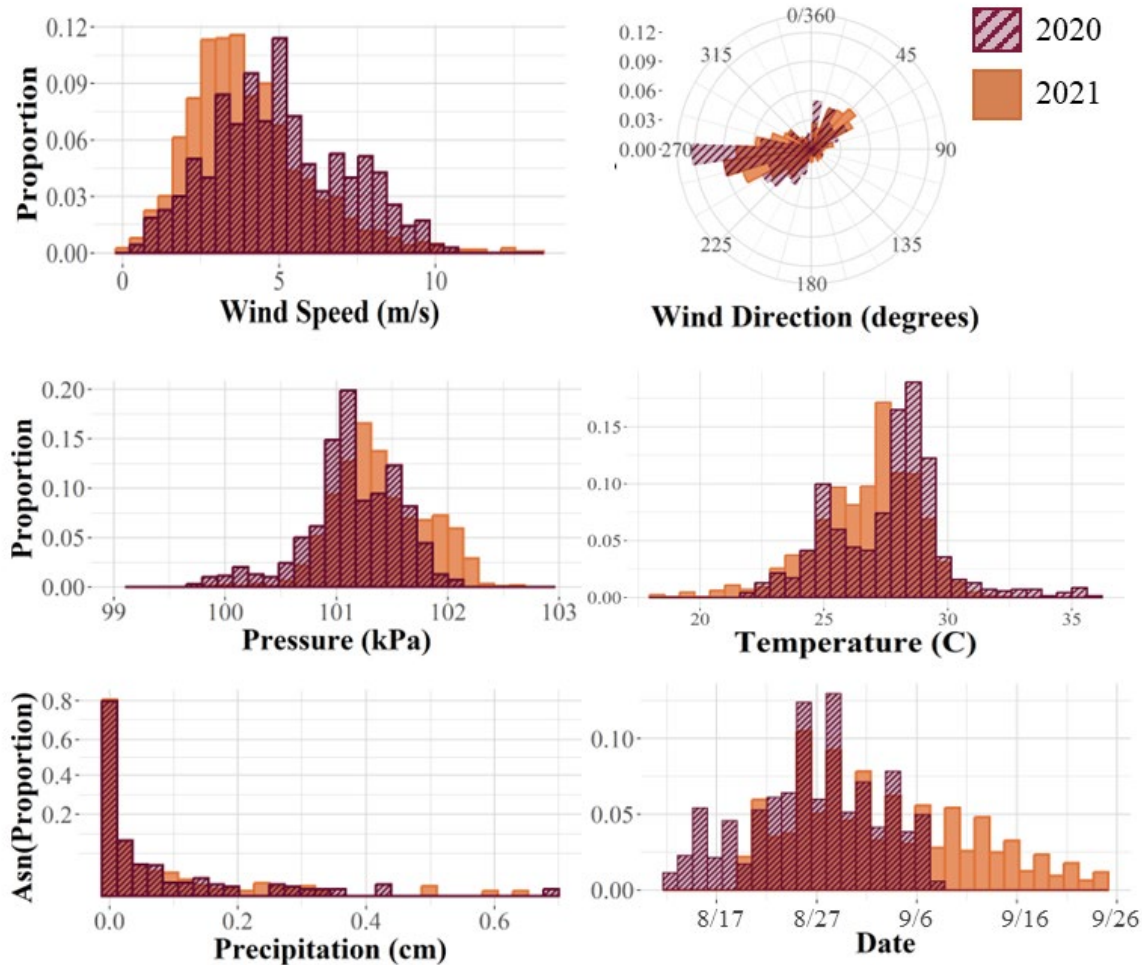


Figure 1. Environmental conditions of raw Red Knot data for individuals tagged in 2020–2021 and included in movement analysis. Weather represents surface level data. General patterns are similar between years though slightly lower wind speeds, more northerly and easterly blowing winds, higher pressure, and later dates in 2021 data.

4.1.1. HMM Model Fit

In examining the influence of environmental covariates on Red Knots comparing offshore and coastal migrants (2021), the models without migrant-movement type interactions performed slightly better (Model 1) than those with migrant-type interactions (Model 2) for both wind speed and direction and wind support (Table 3). Given higher support for wind speed and direction models, the rest of the results focus on these. Given the similarity in AIC values ($\Delta AIC=4$) between Model 1 and Model 2, and the significance of migrant type and various interactions (Table 4), predicted relationships for both models was explored. In examining the influence of environmental covariates on Red Knots comparing between years for offshore migrants (2020-2021), the model with year interactions performed better (Model 4, $AIC=28683$) than the model without interactions (Model 3, $AIC=28700$). Generally, predicted relationships in Model 3 were similar to those for offshore migrants in Model 2, but, as above, regression coefficients

for both models are reported, though the focus here is on predicted environmental relationships that differed between years.

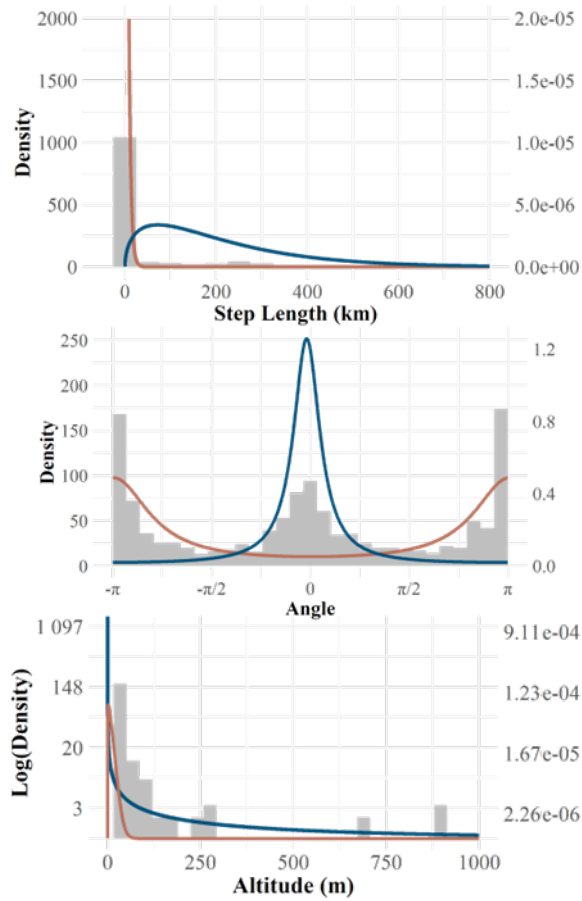


Figure 2. State distributions for the 2021 Red Knot hidden Markov models. Models include two states, staging (red) and migratory (blue), distinguished based on step length (km), turning angle (degrees) and altitude (m). The migratory state is defined by longer more directional movement at higher altitudes compared with the staging state. States are defined consistently across migrant types while geography of movement varies.

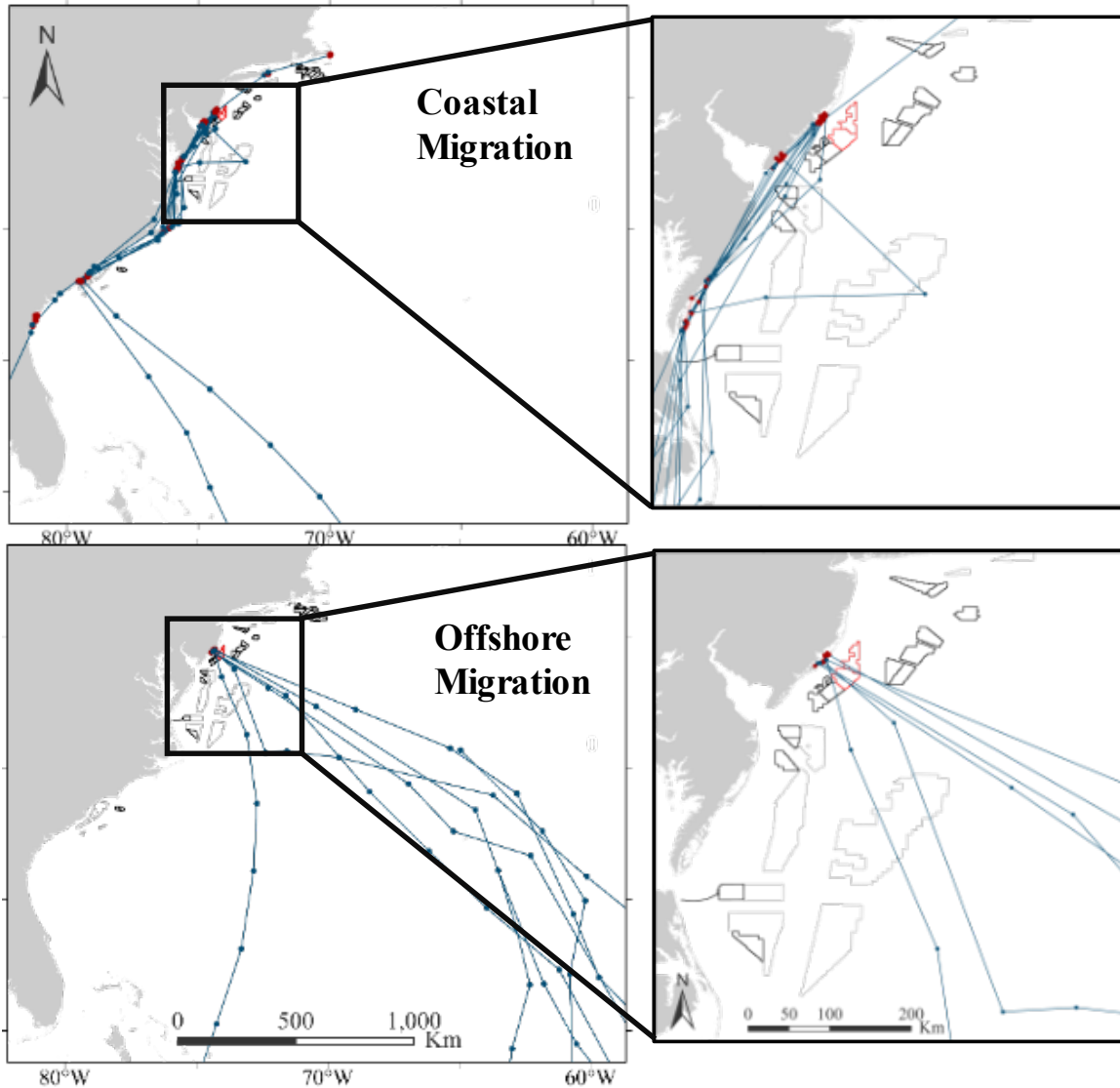


Figure 3. Red Knot state assignments and movement tracks for 2021 data by migrant type (coastal, offshore). State assignments include a migratory state (blue) and staging/non-migratory state (red). Left panel shows full movement patterns, while right panel shows movement in relation to offshore wind lease areas, including Atlantic Shores (red), active leases (black), and planning areas (grey). Coastal migrants exhibit less offshore habitat use as compared with offshore migrants that likely pass through offshore wind lease areas during migration.

Table 3. Red Knot hidden Markov model of 2021 individuals comparing between those with wind speed and direction with those with wind support. Model 1= overall environmental covariates. Model 2= interaction between environmental covariates and migrant type. Based on Akaike's Information Criteria (AIC), there is higher support for models with wind speed and direction.

Model	Wind Covariates	AIC
Model 1	Wind direction + wind speed	38149
Model 1	Wind support	38151
Model 2	Wind direction + wind speed	38153
Model 2	Wind support	38157

4.1.2. Influence of Migrant Type

Across individuals in 2021, in addition to the significance of migrant type in influencing the likelihood of transition from migratory to staging with coastal birds exhibiting a higher transition probability (Prediction: 0.458 [CI: 0.232-0.703]) than offshore migrants (Prediction: 0.194 [0.093-0.361]), evidence indicated that state transitions were significantly influenced by wind speed, wind direction, temperature, date, and time of day (Table 4). In particular, Red Knots were less likely to transition from the migratory to staging state as wind speed increased, and more likely to initiate migratory movement with south-blowing winds (100-200 degrees) and higher temperatures (Figure 4). Additionally, the analysis showed (1) evidence that birds were less likely to switch from a staging to migratory state as date increased, and (2) an influence of time of day (day vs. night) on transition probabilities, whereby birds had a higher probability of switching from a migratory to staging state during the day (Prediction: 0.458 [0.232-0.703]) than at night (Prediction: 0.228 [0.088-0.472]). Though not significant, Red Knots also were more likely to transition from a migratory to staging state as pressure increased, with a particular shift in transition probability between 95–100 KPa and showed a similar pattern with increased precipitation.

There was evidence that migrant types may respond differently to wind characteristics, temperature, and precipitation (Figure 5). In particular, coastal and offshore migrants exhibited marginally different relationships with wind, whereby, as wind speed increased, coastal individuals were less likely to transition from staging to migratory, while offshore migrants were more likely to transition into a migratory state. In contrast, coastal migrants were marginally less likely to switch from migratory to staging as temperature increased, while offshore migrants were more likely to switch. Offshore migrants were significantly less likely to switch to migration as precipitation increased while coastal migrants were seemingly unaffected. Finally, coastal and offshore migrants showed different patterns with time of day (day vs. night) and switching from a migratory state to staging, with coastal migrants were more likely to switch to staging in both the day (Prediction 0.325 [0.120-0.630]) and night (Prediction: 0.298 [0.199-0.569]), in comparison to offshore migrants in both the day (Prediction: 0.003 [0.000-0.513]) and night (Prediction: 0.000 [0.000-0.120]), with the strongest difference between at night, with coastal migrants more likely to switch to staging, while offshore migrants were more likely to remain in a migratory state at night.

Table 4. Red Knot hidden Markov model regression coefficients \pm standard error for 2021 individuals testing the effect covariates on transition probabilities between staging and migratory movement states. Model 1= overall environmental covariates, AIC=38149. Model 2= interaction between environmental covariates and migrant type, AIC=38153. Bolded parameters are significant and italic parameters are marginally non-significant based on confidence intervals. This suggests wind speed, wind direction, temperature, pressure, date, and time of day influence state transitions for all individuals, with variation between offshore migrants with wind speed, temperature, precipitation, and time of day.

Parameter	Model 1		Model 2	
	Staging \rightarrow Migratory	Migratory \rightarrow Staging	Staging \rightarrow Migratory	Migratory \rightarrow Staging
Intercept	-2.34 \pm 0.31	0.13 \pm 0.48	-2.57 \pm 0.43	-0.79 \pm 0.45
Migrant Type	-0.29 \pm 0.35	-1.26 \pm 0.47	0.28 \pm 0.57	-4.44 \pm 2.75
Wind Speed	0.09 \pm 0.18	-0.39 \pm 0.20	-0.21 \pm 0.29	-0.50 \pm 0.31
Temperature	0.28 \pm 0.21	0.12 \pm 0.42	0.67 \pm 0.30	-0.46 \pm 0.54
Pressure	-2.26 \pm 1.23	<i>1.12 \pm 0.86</i>	-2.61 \pm 1.74	2.04 \pm 1.51
Deployment Weight	-0.12 \pm 0.16	-0.16 \pm 0.21	-0.08 \pm 0.25	-0.02 \pm 0.39
Precipitation	-0.14 \pm 0.16	<i>0.25 \pm 0.19</i>	0.09 \pm 0.20	0.33 \pm 0.28
Date	-0.68 \pm 0.21	-0.11 \pm 0.26	-0.84 \pm 0.29	-0.18 \pm 0.39
Time of Day	-0.48 \pm 0.33	-1.05 \pm 0.41	-0.20 \pm 0.44	-0.13 \pm 0.56
Cos(Wind Direction)	-0.70 \pm 0.29	0.13 \pm 0.36	-0.71 \pm 0.39	0.06 \pm 0.53
Sin(Wind Direction)	0.34 \pm 0.24	-0.38 \pm 0.34	-0.32 \pm 0.32	-0.09 \pm 0.50
Wind Speed x Migrant Type			<i>0.73 \pm 0.37</i>	-0.13 \pm 0.49
Temperature x Migrant Type			-0.28 \pm 0.46	<i>1.75 \pm 0.98</i>
Pressure x Migrant Type			0.94 \pm 2.77	-1.01 \pm 2.39
Deployment Weight x Migrant Type			0.11 \pm 0.35	-0.12 \pm 0.49
Precipitation x Migrant Type			-0.73 \pm 0.37	0.21 \pm 0.47
Date x Migrant Type			0.68 \pm 0.45	0.53 \pm 0.57
Time of Day x Migrant Type			-0.82 \pm 0.68	-2.21 \pm 1.03
Cos(Wind Direction) x Migrant Type			-0.18 \pm 0.62	-0.69 \pm 1.01
Sin(Wind Direction) x Migrant Type			0.56 \pm 0.58	-4.62 \pm 2.96

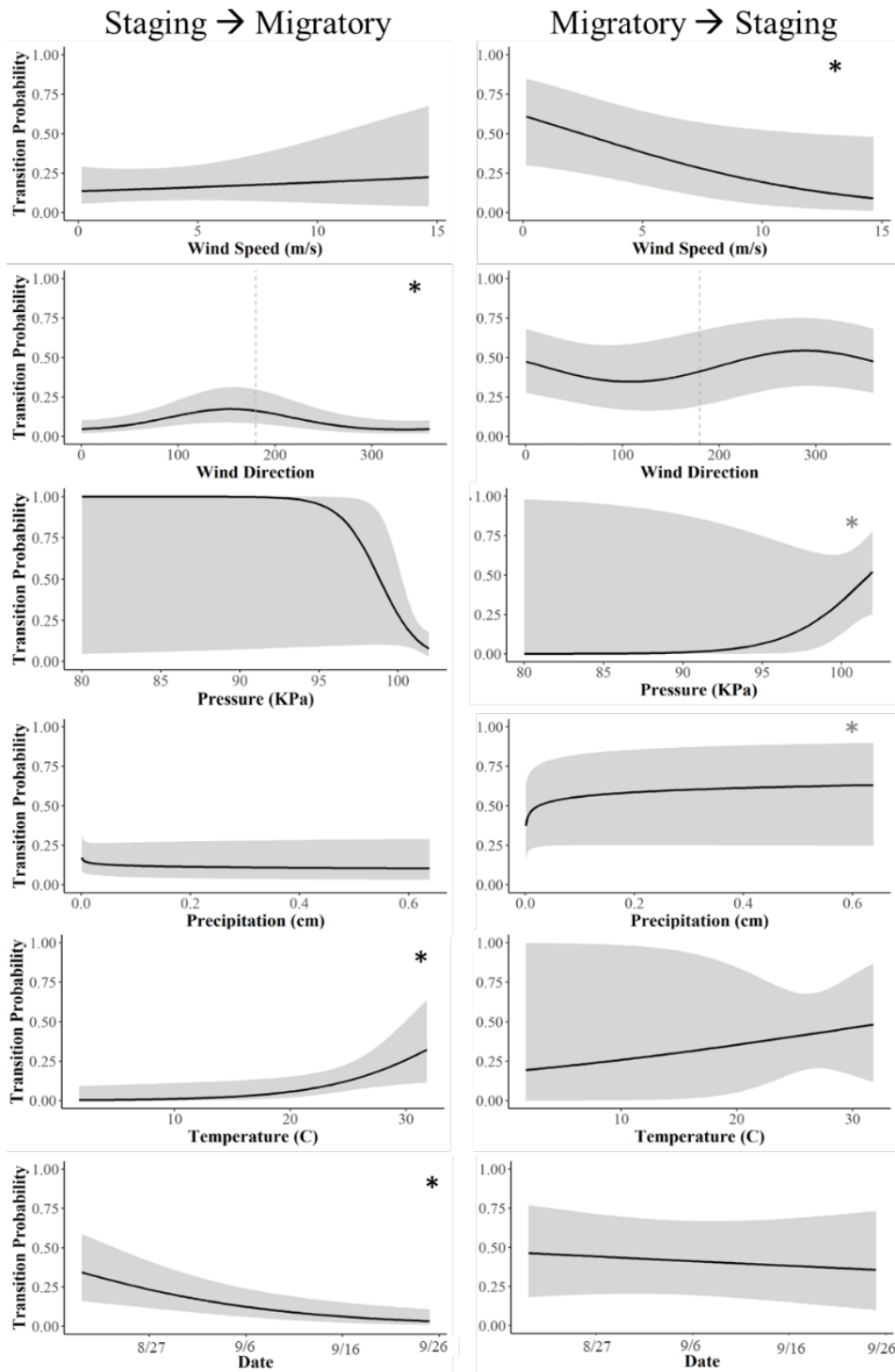


Figure 4. Predicted relationships between environmental variables (wind speed, wind direction, pressure, precipitation, temperature, date) and the transition probabilities of Red Knots (2021) between movement states (staging, migratory). Black stars indicate significant relationships and grey stars indicate marginally non-significant relationships, based on regression coefficients and confidence intervals. Predictions represent relationships for coastal migrants during the day. For wind direction, the horizontal dashed line represents south (180 degree). Red Knots are less likely to switch to staging as wind speed increases and more likely to switch to migrating with southerly wind direction and higher temperature, more likely to switch to staging as pressure and precipitation increases, and less likely to switch to migrating as date increases.

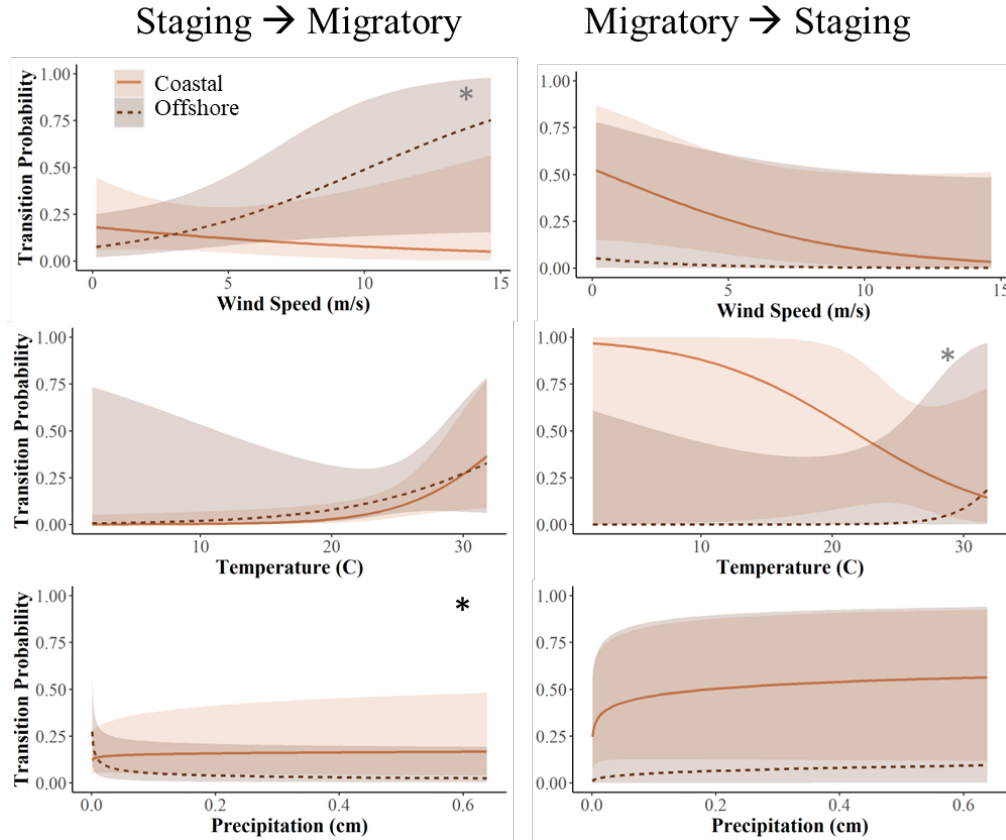


Figure 5. Predicted relationships in the interaction between environmental variables (wind speed, temperature, precipitation) and migrant type (offshore, coastal) and the transition probabilities of Red Knots (2021) between movement states (staging, migratory states). Black stars indicate significant relationships, and grey stars indicate marginally non-significant relationships based on regression coefficients and confidence intervals. Predictions represent relationships during the day. Coastal and offshore migrants differed in their probability of switching between movement states based on wind speed, temperature, and precipitation with offshore migrants more likely to initiate migration with higher wind speeds and lower precipitation, and remain migrating with higher temperatures.

4.1.1. Interannual Variation

In comparing between years, similar overall environmental variables influencing movement patterns as well as evidence for interannual variation (Table 5) was found. Significant differences in transition probabilities between years in relation to wind speed, temperature and pressure (Figure 6) were also identified, with the divergence between years primarily occurring at lower wind speeds (<10 m/s), higher temperatures (>27 °C) and lower pressure (<100 KPa). It is important to note a key difference in the interannual models is the use of surface-level environmental data rather than that at altitude (as for the 2021 models). Additionally, a significant interaction between time of day (day vs. night) and years for the probability of switching from a migratory to staging was noted, whereby, in 2020, Red Knots had a higher probability of switching in the day (Prediction: 0.080 [0.013-0.380]) and night (Prediction 0.179 [0.004-0.526]) compared with 2021 day (Prediction: 0.000 [0.000-0.276]) and night (Prediction: 0.000 [0.000-0.029]), though in all cases the probability was low.

Table 5. Red Knot hidden Markov model regression coefficients \pm standard error for 2020 and 2021 offshore migrant individuals testing the effect covariates on transition probabilities between staging and migratory states. Model 3= overall environmental covariates, AIC 28700. Model 4= Interaction between environmental covariates and migrant type, AIC = 28683. Bolded parameters are significant and italic parameters are marginally non-significant based on confidence intervals. Surface-level wind speed, temperature, and wind direction influenced state transitions for all individuals, with interannual variation in the influence of temperature, pressure, and time of day.

Parameter	Model 3		Model 4	
	Staging \rightarrow Migratory	Migratory \rightarrow Staging	Staging \rightarrow Migratory	Migratory \rightarrow Staging
Intercept	-3.56 \pm 0.42	-3.65 \pm 0.72	-5.64 \pm 1.36	-3.56 \pm 0.79
Year	0.91 \pm 0.46	1.00 \pm 0.47	3.30 \pm 1.39	-18.79 \pm 9.08
Wind Speed	0.52 \pm 0.24	-0.52 \pm 0.24	1.06 \pm 0.54	-0.18 \pm 0.32
Temperature	-0.04 \pm 0.19	0.31 \pm 0.39	-1.25 \pm 0.72	-0.44 \pm 0.60
Pressure	0.09 \pm 0.23	<i>-0.27 \pm 0.17</i>	-0.10 \pm 0.45	-0.16 \pm 0.17
Deployment Weight	0.23 \pm 0.22	-0.12 \pm 0.25	0.34 \pm 0.44	-0.12 \pm 0.45
Precipitation	<i>-0.35 \pm 0.25</i>	0.18 \pm 0.25	-1.07 \pm 0.78	0.29 \pm 0.39
Date	0.13 \pm 0.37	0.09 \pm 0.30	1.76 \pm 1.21	0.22 \pm 0.72
Time of Day	-0.22 \pm 0.40	-0.70 \pm 0.48	1.19 \pm 1.27	0.91 \pm 0.73
Cos(Wind Direction)	0.17 \pm 0.35	-0.50 \pm 0.60	1.47 \pm 0.85	-0.88 \pm 0.95
Sin(Wind Direction)	0.79 \pm 0.33	-1.45 \pm 0.70	0.87 \pm 0.61	-0.74 \pm 0.72
Wind Speed x Year			-0.63 \pm 0.61	-2.74 \pm 0.99
Temperature x Year			1.30 \pm 0.77	4.73 \pm 1.81
Pressure x Year			0.09 \pm 0.53	-2.36 \pm 0.94
Deployment Weight x Year			-0.17 \pm 0.51	0.12 \pm 0.75
Precipitation x Year			0.67 \pm 0.82	-1.25 \pm 0.75
Date x Year			-2.02 \pm 1.26	-1.37 \pm 1.00
Time of Day x Year			-2.25 \pm 1.37	-4.01 \pm 1.37
Cos(Wind Direction) x Year			-1.47 \pm 0.97	4.28 \pm 2.80
Sin(Wind Direction) x Year			-0.50 \pm 0.78	-21.10 \pm 9.39

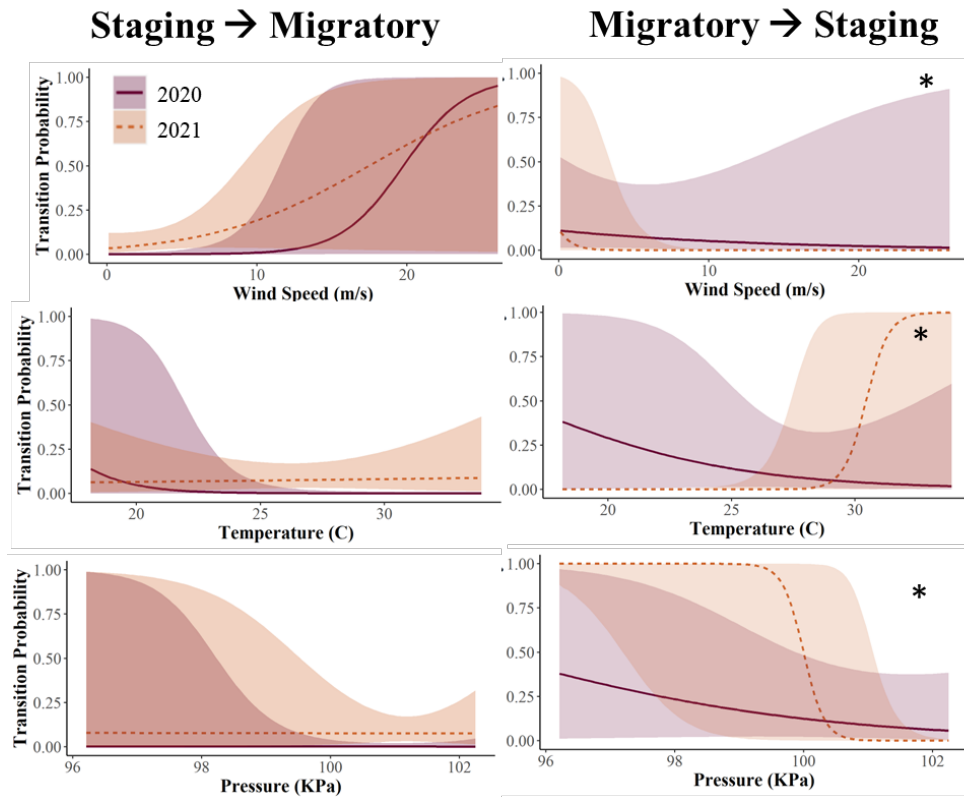


Figure 6. Predicted relationships in the interaction between surface-level environmental variables (wind speed, temperature, pressure) and year (2020, 2021) and the transition probabilities of Red Knots between movement states (staging, migratory states). Black stars indicate significant relationships based on regression coefficients and confidence intervals. Predictions represent relationships during the day. Individuals differed between 2020 and 2021 in transition probabilities, with 2021 individuals probability of switching from migratory to staging increasing with increasing temperature, and decreases with increasing pressure and wind speed compared with 2020 individuals.

4.1. Habitat Use Modeling

4.1.1. Habitat Use of Tracked Individuals

Using kernel density estimation, the space use of the tracked Red Knots in the migratory movement states across region (Figure 7) is illustrated. Migratory strategy (e.g., coastal vs. offshore) was a significant factor in determining space. When in a staging movement state, offshore migrants were observed to exclusively used Mid-Atlantic and South Atlantic coasts, and their movements were generally restricted, while coastal migrants in a staging state used known staging habitats in that region, such as Florida and the Caribbean. Birds in the migratory movement state were found in many different locations, depending on their migratory strategies. The coastal migrants in a migratory state showed some offshore activity but most used routes close to shore through the Caribbean, while offshore migrants in this state avoid land consistently. Examining this habitat use in relation to offshore wind lease areas, the 50% kernel density of both coastal and offshore migrants during migratory movement states showed potential overlap with multiple lease areas, including Atlantic Shores, though offshore migrants exhibited higher density in relation to the Atlantic Shores lease area.

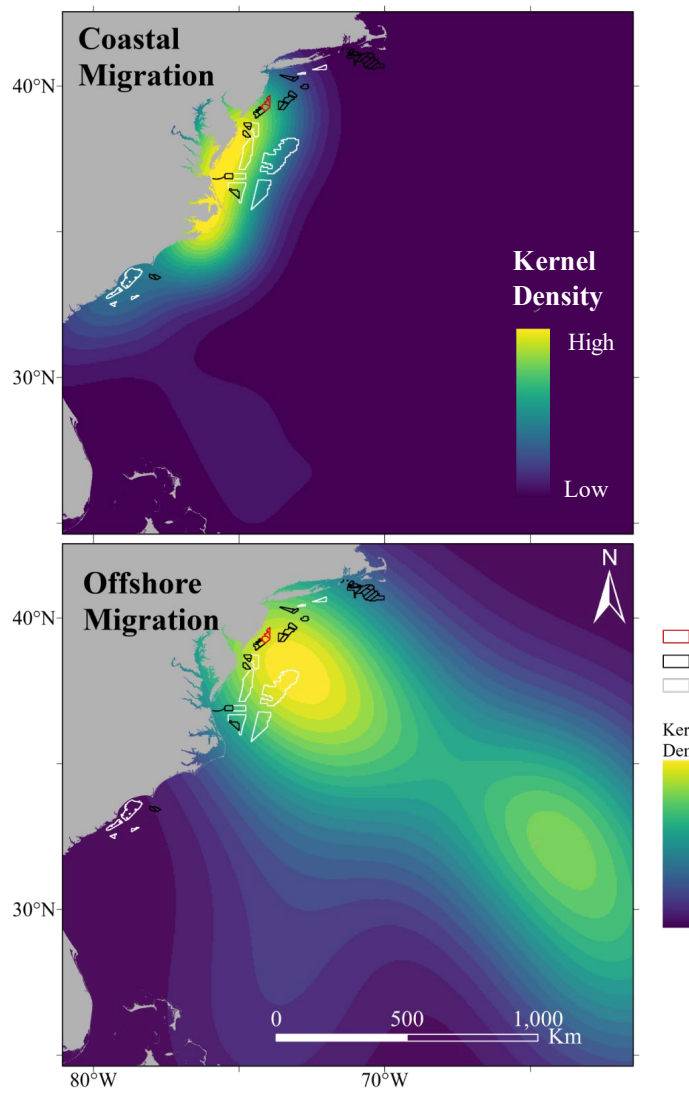


Figure 7. Habitat use of migrating Red Knots determined by kernel density estimation of migratory movement defined based on state assignment from hidden Markov modeling with higher density in yellow and lower density in purple. Coastal migrants were defined as birds that did not cross a significant portion of the Atlantic Ocean in a single migratory flight, and the offshore migrants were the opposite.

4.1.2. SDM Model Fit

After testing multiple models, the final SDM model was selected due to a combination of its simplicity and efficacy. All covariates from Table 1 were included in the model, with no covariates dropped to improve predictive performance. The cross-validation the AUC score was 0.970 (± 0.003), which indicates an excellent fit. There was a strong correlation in predictions with the cross-validation scores as well, 0.910 (± 0.007). As issues with convergence occurred when tree complexity was high, models where tree complexity was limited to 1 all converged easily.

4.1.3. SDM-Predicted Habitat Use

While SDMs can be limited in making causal inference, the variables that were the most important in explaining variation can be illuminating. The most important parameters were distance to shore followed

by altitude (Table 6). Habitat use was variable with distance shore, use was highest immediately offshore and activity decreased until ~1400km offshore. Latitude suggested a bimodal distribution with activity near the staging grounds in New Jersey and winter arrival locations in the Caribbean and Northern South America. Though activity was high throughout the migratory latitudinal range.

Climatology data were not a strong predictor of offshore habitat use. This pattern indicates that weather data at lower temporal scales is more important for predictor habitat use, or that other factors (e.g., individual-level orientation or physiological condition). It should also be noted that covariate importance is not indicative of a causal relationship between occupancy and those predictors.

These covariate relationships were combined to make predictions for the entire study area combining across fall months (August, September) and years based on fall averages of covariates (Figure 8). These predictions show higher offshore habitat use with some use over water during migration to the non-breeding grounds in northern South America. Much of the study area was found to have some level of potential occupancy for migrating Red Knots, emphasizing low-intensity use across the Atlantic past the coastal waters. Activity was also high in coastal areas along North America as migrants of both strategies passed through and used coastal areas for staging. Note that these predictions are based on relatively small amounts of data and some estimates appear inaccurate or an artifact of the model estimation process (e.g., far offshore habitat use predicted near 40N). More data will be helpful for refining these models and improve the model outputs, until these are available we recommend considering these maps has general patterns of potential use and relying on known offshore locations of animals in combination with these predictions to support offshore conservation decisions. When considering habitat use relative to offshore wind development, coastal areas were frequently used by Red Knots, particularly near their departure locations.

Table 6. Relative importance of the top predictive covariates for the Red Knot fall migration species distribution model. Relative influence includes the effect of the covariate itself as well as all interactions with that covariate and all others.

Covariate	Units	Relative Influence
Distance to shore	m	82.6
Latitude	deg	7.7
East/West winds (10 m)	m/s	4.7
Temperature (10 m)	°C	3.4
North/South winds (10 m)	m/s	1.2
Pressure (10 m)	kPa	0.33

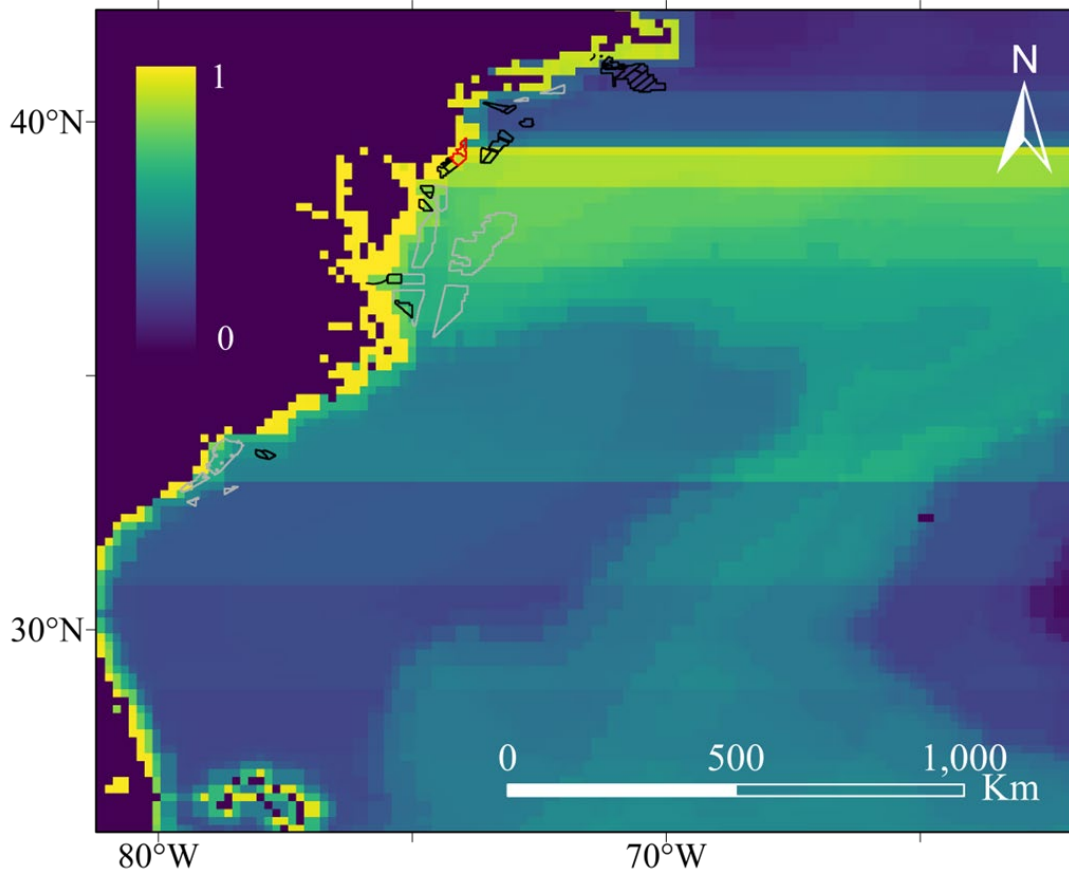


Figure 8. *Predicted occupancy of migrating Red Knots in August/September 2020/2021 from the final SDM model. Values range from 0 (purple) to 1 (yellow). Predictions were made based on fall means of dynamic weather variables and static variables on a 10 km grid system, displayed at 20 km resolution for visualization purposes. Environmental variables were assessed at the centroid of the grid cell. White box represents the region with currently proposed offshore wind energy development. Generally higher predicted occupancy in coastal areas of the Atlantic compared with offshore areas, though occupancy rates are relative the number of pseudo-absences and are only an indicator of relative importance.*

5. Discussion

In examining Red Knot movement patterns and habitat use, evidence for two distinct movement states was identified based on variation in step length (e.g., distance between subsequent locations), turning angle, and altitude. The parameters of these movement states function to support understanding how the potential for interactions with offshore wind development may vary for individuals between these states, particularly for migrating individuals that fly at higher altitudes and greater speed than staging individuals. Flight speed (calculated from step length) and flight height distributions are key to understanding Red Knot exposure and collision risk.

Additionally, movement and environmental variables were used to examine species distributions using two methods, kernel density estimation and species distribution modeling, which provide different perspectives on realized and available habitat use, which can contribute to an understanding of exposure and flux. Finally, environmental variables, in particular wind, pressure, temperature, and precipitation, influenced movement patterns, with variation in patterns between migrant types (coastal, offshore) and years. Understanding the influence of different variables on transition probabilities supports further understanding of the conditions that may lead individuals to initiate and sustain migration, which may influence potential exposure to offshore wind development.

5.1. Influence of weather

Evidence indicated that all individuals, regardless of migration strategy, are less likely to switch from a migratory state to a staging state, and more likely to remain migrating as wind speed increases, likely related to the reduced energy expenditure required when traveling long distances in higher wind. This also relates to wind direction, as tailwinds are more energetically advantageous; all individuals were more likely to initiate migration with wind blowing in a southerly direction (100-200 degrees). In exploring the degree to which wind speed and wind direction compared with tailwinds, we found greater evidence for the importance of wind speed and direction separately. Given that prevailing wind conditions experienced by tracked individuals were primarily southeasterly blowing (180-270 degrees), the interplay between wind speed and direction in this instance may be less important. However, we did find that wind speed influenced movement pattern of offshore migrants more so than coastal individuals, with some evidence of variation between years showing offshore migrants more likely to initiate migration with higher wind speeds in both years. However, in 2021, birds were more likely to remain migrating with high winds when compared with 2020. As offshore migrant individuals must travel further without stopping to refuel, advantageous winds may be particularly important for this movement strategy, though the strength of this relationship appears variable. This hypothesis corresponds with our preliminary findings, whereby individuals showing potential interaction with the offshore lease area (offshore migrants) departed with wind at speeds of at least approximately 5 m/s.

Other environmental variables, including pressure, temperature and precipitation, as well as date, also influenced movement patterns of all individuals, regardless of migrant type. Birds were more likely to initiate and sustain migration with lower pressure (2021). There is evidence that birds are able to detect barometric pressure, and, in turn, use it as a predictor of inclement weather and high winds (Metcalf et al. 2013). Indeed, Sapir et al. (2011) found that migration departure time for European Bee-eaters (*Merops apiaster*) was related to barometric lows that increase the southern component of wind direction. Thus, Red Knots may use cues from pressure changes to take advantage of favorable winds or other beneficial components of weather systems during fall migration. When comparing across years, looking at surface-level pressure for offshore migrants, significant variation was observed. However, the

range of surface-level pressure values was much smaller than when utilizing flight altitude information (2021). This suggests that pressure levels experienced by birds at altitude may be quite different than those at the surface, that interannual variation in this relationship warrants further exploration, and caution should be taken when interpreting relationships between Red Knots and weather in cases where flight height information is not available.

Additionally, an overall pattern was found, whereby increased precipitation leads to a higher likelihood of a switch from migration to staging, suggesting that birds do not like migrating during storms. In addition, offshore migrants were less likely to initiate migration as precipitation increased compared with coastal migrants, suggesting that the avoidance of storms may be more important for birds making large open-ocean flights, whereby opportunities for landing in inclement weather are greatly reduced. Birds are also less likely to switch to a migratory state as the date shifts from August to September, which may relate to the timing of tagging in relation to initiation of migration. Birds initiated migration soon after tagging in August whereby in September they were more likely to remain in a non-migratory/staging state, which is supported by previous knowledge of migration timing for the species in the region (Baker et al. 2020). This suggests that as the migratory season progresses animals are finding their wintering grounds and do not need to engage in further migratory flights.

In examining the relationship between movement patterns and temperature, evidence indicated differences between migrant types and across years. While all individuals were more likely to switch from staging to migrating as temperature increased, sustained migratory movement differed with offshore migrants stopping migration in warmer temperatures while coastal migrants exhibited the opposite pattern. However, the pattern with offshore migrants was only seen in 2021, and not in 2020. In addition, preliminary analysis suggested that offshore individuals initiated migration in warmer temperatures. Taken together, these results suggest that temperature affects migration strategy contextually—as in, some years it may be associated with good migratory conditions, while in others it is not. Relationships with temperature may be correlated with pressure, as previous studies have found White-throated Sparrows (*Zonotrichia albicollis*) respond to changes in both as potential indicators of weather systems (Metcalf et al. 2013). As only two years of data was collected for an interannual comparison in this case, caution should be taken in interpreting differences between years. These should be used more as an indication of higher uncertainty relationships, which warrants further investigation into potential levels of interannual variability.

The findings of this research provide insight into favorable conditions that may contribute to the initiation and sustaining of migratory movement for Red Knots. Thus, risk of exposure to offshore wind lease areas may be higher in instances of these favorable wind conditions (higher speed southerly blowing winds), and related low pressure and precipitation, while the relationship with temperature is less clear. Unsurprisingly, timing also plays a key role, and Red Knots are more likely to initiate migration in August, thus this period, in particular, may also represent greater risk of exposure. Additionally, differences in responses between offshore and coastal migrants and between years was also observed, suggesting that potential risk may vary between migrant types as well as annually; these identified sources of variation should be incorporated into the uncertainty estimates for future risk assessment processes. However, it is important to note that the variables examined in this analysis likely only represent a part of what may contribute to migratory decisions for Red Knots, with other factors related to energetics, stage of molt, and predation pressure playing roles (Beuhler and Piersma 2008, Lank et al. 2003). These aspects should be explored in future analyses.

5.2. Habitat use

Different spatial patterns of habitat use were found when using kernel density estimation and species distribution models, with kernel density estimates showing high densities in coastal areas for staging and migration of coastal individuals, and greater use of pelagic habitats for offshore migrants. In contrast, the SDM predictions showed consistent habitat use close to the coast and with less concentrated activity overwater.

The two approaches to modeling distributions describe different types of space use. Using a kernel density estimator, only habitat use for areas where birds were directly observed can be considered, though this provides insight into relative differences in densities between migrant types and movement states. These results provide an interesting contrast to the machine learning SDM techniques, which build complex predictive models and associate patterns of occupancy with environmental covariates throughout the offshore range of the species. The predictions from these models generalize the habitat use patterns detected from the migration tracks using covariate associations. Thus, habitat that they could use but were not observed using can be identified as important using this approach, which contrasts with the kernel density methods. A useful analogy is thinking of these two analyses as estimates of a realized and fundamental spatial niche – though the realized niche is necessarily biased by the individuals that were observed, while the fundamental niche assesses all possible habitat for all individuals. When considering how to apply this information to decisions, if a stakeholder is interested in areas where the tracked individuals used habitat, the kernel density approach is the most useful, while the SDM approach identifies habitat that animals could—and should—utilize during staging and migration. Thus, these represent two different approaches for how habitat use may be understood, and, in turn, exposure to offshore wind energy development. Indeed, both could be used together to represent different aspects of flux in collision risk modeling, which would provide an opportunity to incorporate uncertainty and understand how different biases may be contributing to outcomes.

5.3. Future Studies

Initial evidence for differences in movement patterns and responses for offshore and coastal migrants was found, as well as interannual variability in relationships with environmental variables; these relationships warrant further investigation. In particular, little is known about the degree of fidelity in migration strategy for a given individual across years, and how much local environmental conditions contribute to the frequency of the offshore migration strategy. Given that migration strategy contributes greatly to potential exposure to offshore wind development sites, the proportion of the population exhibiting these two strategies, in addition to understanding interannual variability, will be key in understanding risk. Currently, studies have been attempting to preferentially tag animals that would migrate offshore, so more data would be needed to estimate the frequency of these strategies across the entire population.

As mentioned above, altitude information may be essential in disentangling sources of variation in relationships with environmental variables, particularly those that may vary greatly with altitude (i.e., pressure). Thus, the collection of 3D movement information may be key as work is undertaken to gain further clarity in these relationships. It is also important to note that the movement modeling was hindered by data collection protocols, whereby the 2020 data was not collected at a consistent time step, which is a central assumption in HMM analyses. This led to the need to implement CRWM smoothing to facilitate an interannual comparison, which both hindered the ability to incorporate altitude information (and weather at altitude) and led to additional assumptions about how birds were moving through space.

Thus, the interannual models should be interpreted with caution, and careful consideration should be given in determining sampling frequency for future tracking if there are intentions to implement discrete-time movement modeling.

Finally, it is important to recognize the limitations of both habitat modeling approaches. As both habitat modeling approaches use tracking data, both may also be affected by spatiotemporal autocorrelation in the data, explicitly accounting for this in analysis could improve accuracy of these models (Silva et al. 2021, Guelat and Kery 2018) and should be explored in future studies. In addition, the kernel density approach represents a coarse spatial tool and is fundamentally limited by sample size and collecting large amounts of data to describe population-level movement patterns accurately. The SDM approach has limitations as well, as there are potential sources of bias in the model-fitting process and overfitting can occur and bias model predictions. While some of these sources of error have been controlled here (including overfitting), more data would help to ameliorate overfitting issues and provide a more robust estimate of offshore habitat use that account for a wider range of individuals. Another potential source of bias lies in pseudo-absence generation (Hazen et al. 2021). Generating pseudo-absences across the broader study area is useful for identifying large-scale patterns, we are likely missing meso-scale changes in occupancy and potential differences in habitat use among migrant types. As such, caution should be used with the model predictions at smaller spatial scales. Future SDM analysis of migratory habitat use for species should explore additional methods of pseudo-absence generation.

5.4. Conclusions

This analysis provides important insights into Red Knots movement patterns, habitat use, and sources of variation in those relationships. The associated findings have the potential to inform various aspects of future risk assessment for the species in regard to offshore wind development. Specifically, the movement parameters from the HMMs can inform aspects of exposure and vulnerability risk that Red Knots face from ocean development throughout their migratory range. The parameters for the migratory movement state are particularly relevant, as it is during this type of movement that Red Knots appear more likely to interact with planned offshore wind development. In addition, the associated estimates of habitat use (both realized use from the kernel density estimates and predicted occupancy from the SDM) can be used to inform potential flux rates and show higher activity levels around WEAs in the region. By examining differences in migrant type and years, as well as the influence of environmental conditions, an understanding of potential variability in these different aspects of risk and particularly periods or conditions where risk is higher can be built.

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