Atmospheric and spatial drivers of egg abundance in beach nesting shorebirds across an urban-coastal gradient of the Rockaway Peninsula, New York

By

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Abstract

Understanding the drivers of reproductive patterns in beach-nesting shorebirds is essential for conservation in dynamic coastal systems. This study evaluated the influence of atmospheric, geomorphological, and anthropogenic factors on egg abundance and nesting patterns across four distinct areas of the Rockaway Peninsula, New York. Descriptive analyses revealed clear spatial structuring of nesting communities. Colonial species (Common Tern and Least Tern) formed dense aggregations, whereas territorial species (Piping Plover and American Oystercatcher) maintained greater spacing among nests. Nest placement relative to the high tide line, vegetation, and human infrastructure reflected trade-offs among flooding risk, predator detection, habitat availability, and disturbance. A Poisson generalized linear model identified maximum temperature as the dominant factor associated with egg abundance, showing a consistent negative relationship. Elevation had a significant and positive but secondary effect, likely related to reduced flooding risk and higher nesting locations. These patterns were consistent across complementary modeling approaches, including Random Forest analysis. Overall, thermal conditions and coastal microtopography emerged as key determinants of reproductive patterns, highlighting the sensitivity of shorebirds to warming and the importance of maintaining suitable nesting habitat in urbanized coastal systems.

1. Introduction

Shorebirds have long served as important systems for studying ecological and evolutionary processes, yet they are among the most rapidly declining avian taxa worldwide, particularly in North America (Székely, 2019; Smith et al., 2023). A landmark continental assessment estimated a net loss of approximately 2.9 billion birds in North America since 1970, a 29% reduction in total abundance, including a 37% decline in shorebirds (Rosenberg et al., 2019). More recent analyses indicate that these losses are not only widespread but accelerating in multiple regions, particularly in areas associated with agricultural intensification and climatic warming (Leroy et al., 2026). Climate-driven sea-level rise and increasing coastal storm intensity are projected to further reduce available nesting habitat and increase flood exposure for beach- and estuary-dependent species, amplifying their vulnerability under future climate scenarios (Galbraith et al., 2014). Collectively, this evidence indicates that anthropogenic environmental change is intensifying both the scale and rate of avian population declines.

Beyond continental assessments, long-term local monitoring programs have documented substantial declines at key estuarine sites. For example, wintering shorebird abundance declined by 66% over three decades in coastal California, with rainfall variability and habitat restoration influencing interannual dynamics (Warnock et al., 2021). These regional trends reflect the combined effects of habitat loss across breeding, migratory, and wintering grounds, increasing anthropogenic disturbance in coastal environments, climate-mediated shifts in habitat suitability, and emerging infectious diseases such as highly pathogenic avian influenza (Ramey et al., 2022; Klaassen & Wille, 2023; Caliendo et al., 2024; Swayne et al., 2024). Migratory shorebirds, particularly those breeding at high latitudes, appear disproportionately affected due to cumulative pressures along migration routes and heightened sensitivity to environmental change (Koleček et al., 2021). Despite extensive documentation of abundance trends, the demographic mechanisms underlying these declines remain insufficiently resolved. Population trend estimates are sensitive to model structure and assumptions, underscoring the need for analytical frameworks capable of capturing non-linear dynamics across space and time (Smith & Edwards, 2021). However, comparatively fewer studies have examined how fine-scale climatic, geomorphological, and anthropogenic variation influences reproductive parameters in heterogeneous urban-coastal systems.

Reproductive output is a central demographic mechanism underlying population persistence, as variation in fecundity and recruitment can strongly influence population trajectories under environmental change (Sæther & Engen, 2015). Migratory shorebirds face multiple interacting threats across their annual cycle, including pressures that may affect reproductive success (Pearce-Higgins et al., 2017). In beach-nesting shorebirds, clutch size reflects the integration of physiological constraints, habitat quality, disturbance regimes, temperature extremes, and exposure to coastal flooding associated with low elevation and storm

processes (Galbraith et al., 2014; Maslo et al., 2018; van de Ven et al., 2019). Nonetheless, the combined and relative effects of these drivers on egg abundance are incompletely understood in heterogeneous urban-coastal systems.

Along the Atlantic Coast of North America, several beach-nesting shorebirds are listed as threatened or of conservation concern. Among these, the Piping Plover (*Charadrius melodus*), American Oystercatcher (*Haematopus palliatus*), Least Tern (*Sternula antillarum*), and Common Tern (*Sterna hirundo*) occur along the Rockaway Peninsula, New York City, and form the focal species of this study (New York State Department of Environmental Conservation, 2026; US Fish and Wildlife Service, 2026). The Rockaway Peninsula provides a natural laboratory for examining these dynamics within a single barrier system encompassing contrasting geomorphological conditions and levels of urbanization (Figures 1-2). The peninsula includes a managed urban beach sector (Beach 37th St.-56th St.), a semi-natural protected site (Fort Tilden), an exposed ocean-facing system (Breezy Point Ocean Side), and a sheltered estuarine environment (Breezy Point Bay Side), forming a gradient of habitat configuration and disturbance intensity.

The objective of this study is to evaluate how spatial, environmental, and atmospheric variables are associated with variation in egg abundance across these geomorphologically distinct nesting sites. Specifically, this study addresses the following questions: (1) Which spatial, environmental, and atmospheric factors most strongly explain variation in egg abundance? (2) How do these relationships reflect differences in habitat suitability among nesting sites? (3) Does a dominant driver emerge when relationships are evaluated using both parametric and non-parametric modeling frameworks? It is hypothesized that climatic and geomorphological factors, particularly temperature and elevation, exert measurable effects on egg abundance through both physiological constraints and habitat-mediated mechanisms. These hypotheses are tested using a combination of regression-based statistical models and machine-learning approaches, enabling formal inference while assessing predictor importance under flexible modeling structures.

Figure 1. Study Area: Rockaway Peninsula, Queens, New York City.

Figure 2. Nesting points at: a) Beach 37th St.-56th St., b) Fort Tilden, c) Breezy Point Ocean Side, and d) Breezy Point Bay Side.

2. Study Area

The Rockaway Peninsula, located in Queens, New York City, forms a barrier beach system along the Atlantic coast and constitutes the southern boundary of Jamaica Bay. The peninsula is part of the broader chain of barrier islands extending along the southern shore of Long Island and the eastern seaboard of North America. Its geomorphology reflects long-term coastal processes driven by wave action, littoral drift, and sediment redistribution, which have promoted westward barrier growth and the formation of sandy beaches, dunes, and tidal habitats (Sanderson, 2016; Greenlees, 2020). These processes continue to shape shoreline morphology and sediment availability, producing substantial spatial variability in beach width and coastal structure over relatively short distances (Wei & Miselis, 2022; Janda et al., 2025).

Barrier island systems such as the Rockaway Peninsula are inherently dynamic and shaped by interactions among geological framework, hydrodynamic forcing, and sediment supply. Variability in shoreface morphology and sediment thickness contributes to differences in beach stability and shoreline change rates, influencing how coastal segments respond to storms and sea-level rise (Wei et al., 2021; Wei & Miselis, 2022). Along the south shore of Long Island, longshore sediment transport generally moves from

east to west, promoting sediment accumulation near the western end of the peninsula while other segments experience more moderate shoreline change (Janda et al., 2025). These processes are further modified by coastal engineering structures, nourishment projects, and other human interventions that alter sediment fluxes and shoreline morphology.

Beyond natural coastal dynamics, the peninsula lies within one of the most densely populated metropolitan regions in the world. Urban development, coastal infrastructure, and recreational use have substantially modified portions of the coastline while leaving other segments relatively undeveloped. Human alterations to Jamaica Bay, including dredging, inlet stabilization, and land reclamation, have modified hydrodynamics and storm tide propagation, increasing sensitivity to storm surge and coastal flooding (Orton et al., 2020). Consequently, coastal ecosystems in the peninsula reflect a complex interaction between geomorphic processes and anthropogenic pressures.

The system is also highly vulnerable to coastal hazards. Barrier beaches within the Gateway National Recreation Area exhibit varying susceptibility to shoreline change, overwash, and sea-level rise depending on local geomorphology, coastal slope, wave exposure, and historical shoreline change rates (Pendleton et al., 2005). Extreme events such as hurricanes and nor'easters can produce substantial coastal erosion, storm-surge flooding, and rapid morphological change, processes often amplified in densely developed coastal regions of the northeastern United States (Coch, 2015).

Within this heterogeneous coastal landscape, four nesting sites were selected to represent contrasting environmental conditions and levels of human influence along the peninsula. In combination, these sites capture a gradient of geomorphological exposure, habitat configuration, and anthropogenic disturbance that enables examination of spatial variation in nesting ecology within a single urban barrier island system:

a) **Beach 37th St.-56th St.** represents a managed urban beach sector characterized by wide sandy beaches, low dune systems, and high recreational use. Although intensively maintained for public access, the site retains open sandy substrates suitable for beach-nesting shorebirds. Nesting habitat is strongly influenced by proximity to infrastructure, boardwalks, and pedestrian access, making this the most urbanized portion of the study system. Previous monitoring indicates that nesting often occurs within relatively small sections of shoreline where management actions such as fencing and symbolic barriers are implemented to reduce disturbance (Arndtsen, 2022).
b) **Fort Tilden**, located within the Gateway National Recreation Area, comprises a semi-natural coastal landscape including oceanfront beach, dune systems, maritime vegetation, and adjacent wetlands. Compared with the urban sector, infrastructure density and human disturbance are lower, and dune

systems are more structurally developed. Coastal protection structures have been implemented in parts of this site to mitigate storm impacts and protect natural and cultural resources (Bearmore et al., 2016).

c) **Breezy Point Ocean Side** represents a largely undeveloped and highly exposed ocean-facing environment at the western tip of the peninsula. The site contains extensive dune systems and wide beaches shaped primarily by Atlantic wave action and storm-driven processes. Sediment accumulation is influenced by longshore transport and coastal structures such as the Breezy Point jetty, which historically altered patterns of westward barrier growth (Pendleton et al., 2005; Greenlees, 2020).

d) **Breezy Point Bay Side** contrasts strongly with the ocean-facing zones, bordering the sheltered waters of Jamaica Bay. This environment is characterized by tidal flats, salt marshes, and narrower sandy margins reflecting estuarine geomorphology rather than open-ocean exposure. Nesting habitat is more spatially constrained than on ocean-facing beaches, and the bay system has experienced substantial geomorphic change and wetland loss over the past century due to both natural processes and human modification (Sanderson, 2016; Orton et al., 2020).

Together, these four study sites form a gradient of geomorphological exposure, sediment dynamics, habitat configuration, and anthropogenic pressure. This gradient provides an opportunity to examine how environmental conditions and landscape structure influence the spatial ecology and reproductive investment of beach-nesting shorebirds within a single metropolitan coastal system.

3. Regression Modeling and Machine Learning Approaches

Statistical modeling provides a fundamental framework for analyzing ecological data and understanding how environmental variables influence biological responses. Regression models allow researchers to evaluate the relationship between a dependent variable and one or more explanatory variables by estimating how changes in predictors are associated with variation in the response variable. In ecological research, regression approaches are widely used to quantify the influence of environmental factors on demographic responses such as abundance, survival, or reproductive output (Montgomery et al., 2012).

Traditional regression methods are generally hypothesis-driven and rely on explicit assumptions regarding the functional form of relationships, the distribution of errors, and the independence of observations. While these models offer strong interpretability and inferential clarity, ecological systems often involve complex interactions, environmental heterogeneity, and non-linear responses that may not be fully captured by simple parametric models. For this reason, modern ecological analyses frequently combine classical statistical models with more flexible approaches, including generalized regression frameworks and machine learning methods, which allow patterns to emerge from the data with fewer a priori assumptions (Hastie et al., 2009).

3.1. Multiple Linear Regression and Model Diagnostics

Multiple Linear Regression (MLR) extends simple regression by incorporating two or more independent variables to explain variation in a dependent variable. Its general form is expressed as:

$$Y_i = \beta_0 + \beta_1 X_{1i} + \beta_2 X_{2i} + \cdots + \beta_n X_{ni} + \epsilon_i$$

where Y_i is the response variable for observation i, β_0 is the intercept, β_k are the regression coefficients associated with each predictor variable X_k, and ϵ_i is the error term. In practice, the parameters of multiple regression models are typically estimated using the Ordinary Least Squares (OLS) method, which determines the values of the coefficients that minimize the sum of squared residuals between observed and predicted values. Model performance in OLS can be evaluated using several complementary statistics that describe the explanatory power and parsimony of the model. The coefficient of determination R^2 represents the proportion of variance in the dependent variable explained by the predictor variables, while the adjusted R^2 accounts for the number of predictors included in the model and penalizes unnecessary complexity. Model selection can also be evaluated using the Akaike Information Criterion (AIC), which compares the relative quality of competing models by balancing goodness-of-fit and model complexity, with lower AIC values indicating more parsimonious models (Gujarati & Porter, 2009). Reliable inference, however, depends on the adequacy of several diagnostic assumptions that help assess the validity and stability of regression estimates:

a) **Normality of the residuals.** It involves evaluating whether model residuals follow an approximately normal distribution. Normality facilitates valid statistical inference by ensuring that hypothesis tests and confidence intervals behave as expected. The Shapiro-Wilk test is widely regarded as one of the most powerful methods for detecting deviations from normality across different sample sizes (Shapiro & Wilk, 1965). Comparative analyses have demonstrated that the Shapiro-Wilk test generally outperforms alternative procedures such as the Kolmogorov-Smirnov, Lilliefors, and Anderson-Darling tests in statistical power (Razali & Wah, 2011). For this reason, it is frequently recommended as a reliable diagnostic tool in statistical modeling (Ghasemi & Zahediasl, 2012).
b) **Homoscedasticity.** It refers to the assumption that the variance of the residuals remains constant across levels of the independent variables. When this assumption is violated, heteroscedasticity may arise, potentially affecting the reliability of standard errors and statistical inference. The Breusch-Pagan test is commonly used to detect heteroscedasticity in regression models estimated by OLS. This procedure evaluates whether the variance of the residuals is systematically related to the explanatory variables by regressing the squared residuals on the predictors (Gujarati & Porter, 2009).

c) **Independence of errors.** Regression models also assume that residuals are independent from one another. Violations of this assumption may occur when observations are correlated across time or space, generating autocorrelation that can bias the results (Durbin & Watson, 1950). The Durbin-Watson statistic is commonly used to evaluate potential autocorrelation in model residuals. Values between approximately 1.5 and 2.5 generally indicate the absence of significant autocorrelation, suggesting that the residuals can be considered independent.

d) **Multicollinearity.** It occurs when two or more explanatory variables are strongly correlated with each other. High multicollinearity can inflate the variance of regression coefficients, making parameter estimates unstable and difficult to interpret. The Variance Inflation Factor (VIF) is widely used to assess multicollinearity. Values below 5 are generally considered acceptable, whereas values above 10 indicate severe multicollinearity that may require removing or combining variables (Montgomery et al., 2012). Although multicollinearity does not necessarily reduce predictive performance, it can complicate the interpretation of individual coefficients (Gujarati & Porter, 2009).

However, many ecological response variables do not satisfy the assumptions required for classical linear regression. Variables such as nest counts or reproductive output often consist of discrete counts that follow non-normal distributions. For this reason, GLMs provide a more appropriate framework for modeling ecological count data.

3.2. Generalized Linear Models for Ecological Count Data

GLMs extend classical regression by allowing the response variable to follow probability distributions from the exponential family, such as the Poisson, binomial, or gamma distributions. GLMs consist of three main components: a probability distribution for the response variable, a linear predictor that combines explanatory variables, and a link function that relates the expected value of the response variable to the linear predictor. Parameters in GLMs are typically estimated using Maximum Likelihood Estimation (MLE), which identifies the set of coefficients that maximizes the probability of observing the data given the specified model (McCullagh & Nelder, 1989). When modeling count data, the Poisson distribution is commonly used because it describes the probability of observing a given number of events within a fixed spatial or temporal interval (Montgomery et al., 2012).

In a Poisson regression model, the expected value of the response variable is related to the predictors through a logarithmic link function:

$$\log(\mu_i) = \beta_0 + \beta_1 X_{1i} + \beta_2 X_{2i} + \cdots + \beta_n X_{ni}$$

where μ_i represents the expected count. The logarithmic link ensures that predicted values remain strictly positive, a necessary property when modeling count data (Montgomery et al., 2012). In a Poisson regression

model with a log link, the coefficients β_k represent the change in the logarithm of the expected count associated with a one-unit increase in the corresponding explanatory variable. Exponentiating these coefficients yields incidence rate ratios, which capture the multiplicative effect of the covariates on the expected count (Cameron & Trivedi, 2013).

A central assumption of the Poisson model is equidispersion, meaning that the conditional mean and variance of the response variable are equal. However, ecological datasets frequently exhibit overdispersion, a condition in which the variance of the response variable exceeds its mean. Overdispersion can lead to underestimated standard errors and inflated statistical significance if not properly addressed (Hilbe, 2011). To evaluate potential overdispersion, dispersion statistics can be calculated using the ratio of the residual deviance or the Pearson chi-square statistic to the residual degrees of freedom. Values close to one indicate consistency with the Poisson assumption, whereas substantially larger values suggest overdispersion (Cameron & Trivedi, 2013). When overdispersion is present, alternative models such as negative binomial regression may be considered because they incorporate an additional dispersion parameter to accommodate greater variance (Hilbe, 2011).

Even when dispersion diagnostics do not indicate strong violations of model assumptions, ecological data may still contain unobserved heterogeneity or mild model misspecification. For this reason, heteroskedasticity-consistent or robust standard errors are often employed as a conservative approach to statistical inference. Robust variance estimators adjust the estimation of standard errors without altering coefficient estimates or fitted values, allowing statistical inference to remain valid under a wider range of conditions. They are appropriate even when diagnostic tests do not indicate strong violations of model assumptions, as they reduce the risk of overstated statistical significance without affecting substantive conclusions (White, 1980; McCullagh & Nelder, 1989; Cameron & Trivedi, 2013).

Because GLMs do not rely on variance decomposition through sums of squares, the classical coefficient of determination used in linear regression is not directly applicable. Instead, goodness-of-fit is often assessed using pseudo-R^2 measures that compare the likelihood of the fitted model with that of a null model containing only an intercept. The Cox and Snell pseudo-R^2 is one such metric and reflects the improvement in model likelihood achieved by incorporating explanatory variables (Cameron & Trivedi, 2013). In ecological count data models, pseudo-R^2 values are often relatively modest due to the inherent variability of ecological processes, where pseudo-R^2 values between approximately 0.10 and 0.30 are common (Hilbe, 2011). These pseudo-R^2 measures do not represent the proportion of variance explained and therefore are not directly comparable to the R^2 statistic used in linear regression models.

Although Poisson GLMs provide a flexible framework for modeling ecological count data, certain characteristics of ecological datasets may require additional modeling approaches. For example, hierarchical sampling designs, grouped observations, or complex non-linear relationships between environmental variables and biological responses may not be fully captured by standard GLMs. In such cases, alternative regression frameworks, such as Generalized Linear Mixed Models (GLMMs) and Generalized Additive Models (GAMs), can provide additional flexibility for modeling ecological processes (McCullagh & Nelder, 1989; Bolker et al., 2009).

3.3. Alternative Regression Frameworks

GLMMs extend the GLM framework by incorporating both fixed and random effects, allowing the analysis of non-Gaussian response variables while accounting for hierarchical or grouped data structures. Fixed effects represent the average influence of predictors on the response variable, whereas random effects capture variability among groups such as sites, species, or individuals. GLMMs are particularly valuable in ecological studies where observations are not fully independent due to spatial or hierarchical sampling designs. By explicitly modeling group-level variation, GLMMs can provide more realistic representations of ecological processes and improve the generalizability of model results (Bolker et al., 2009). However, the reliability of random-effect variance estimates depends on the number of levels within the grouping factor. When the number of groups is small (typically fewer than five or six levels), estimates of between-group variance may become imprecise or unstable, potentially leading to convergence issues or unreliable inference (Bolker et al., 2009; Harrison et al., 2018). These problems may be exacerbated when the number of observations per group is highly unbalanced. For this reason, when grouping factors include few levels, it is often recommended to treat them as fixed effects or to interpret random-effect variance estimates with caution (Harrison et al., 2018; Gomes, 2022).

Meanwhile, GAMs represent another extension of the GLM framework that allows non-linear relationships between predictors and the response variable using smooth functions (Hastie et al., 2009; S. N. Wood, 2017). Instead of imposing a strictly linear relationship, GAMs estimate flexible smoothing functions that can capture complex ecological responses along environmental gradients. These models are particularly useful when biological responses vary non-linearly with environmental conditions such as temperature, elevation, or habitat structure. However, the increased flexibility of GAMs may reduce interpretability and require sufficient sample sizes and coverage across predictor ranges to estimate smooth functions reliably. When GAMs do not substantially improve model fit or alter the qualitative interpretation of predictor effects relative to simpler parametric models, their use may be unnecessary. In such cases, retaining a more parsimonious model can facilitate interpretation and communication of results while preserving inferential clarity (S. N. Wood, 2017).

Even though extensions of GLMs such as GLMMs and GAMs provide considerable flexibility for modeling hierarchical structure and non-linear responses, they still rely on parametric assumptions about the functional relationships between predictors and the response variable. In ecological systems characterized by complex interactions, high-dimensional predictors, or unknown functional forms, machine learning approaches can offer an alternative framework for exploring patterns in the data. These methods prioritize predictive performance and can capture complex relationships without requiring explicit specification of the model structure.

3.4. Machine Learning Approaches in Ecological Modeling

Among machine learning methods, Random Forest (RF) is one of the most widely used algorithms for ecological prediction and variable importance assessment. RF is an ensemble learning algorithm that constructs many decision trees using bootstrap samples of data and random subsets of predictors. Predictions are obtained by aggregating the results of individual trees, which reduces variance and improves predictive stability compared to single decision trees. Because RF does not require assumptions about linearity, distributional form, or specific functional relationships between variables, it can capture complex interactions and non-linear responses commonly observed in ecological systems. In addition, RF internally estimates predictive error using out-of-bag (OOB) samples, providing an unbiased assessment of model performance without requiring an independent validation dataset (Hastie et al., 2009).

In addition to generating predictions, RF models can also provide estimates of variable importance. One widely used metric is permutation importance, which evaluates the contribution of each predictor by measuring the decrease in predictive accuracy when the values of that variable are randomly permuted while all other variables remain unchanged. Predictors whose permutation produces larger decreases in predictive accuracy are interpreted as having greater influence on model performance (Fisher et al., 2019). By evaluating variable importance within a flexible, non-parametric framework, RF helps identify dominant predictors and assess whether patterns detected by parametric regression models remain consistent when strict parametric assumptions are not imposed.

4. Data and Methods

4.1. Description of measurements

This section outlines the methodological framework used to quantify spatial, environmental, and atmospheric variables associated with shorebird nesting along the Rockaway Peninsula during the 2025 breeding season. Measurements were designed to ensure high spatial accuracy while minimizing disturbance to nesting birds and preserving the integrity of sensitive reproductive processes. Data collection

integrated field-based geospatial measurements, remote sensing analysis, tidal assessments, atmospheric datasets, and geomorphological calculations to comprehensively characterize nesting habitat conditions.

4.1.1. Nesting points monitoring and data collection

Nesting monitoring was conducted weekly over a 15-week period from late April to early August 2025. Surveys covered four focal stretches: Beach 37th St.- 56th St., Fort Tilden, Breezy Point Ocean Side, and Breezy Point Bay Side, totaling approximately 15 observation hours per site across the breeding season. The objective was to precisely identify and geolocate shorebird nests while minimizing human disturbance.

Upon first detection of a new nest, a rangefinder was used to determine distance relative to pre-established seasonal beach nest markers (installed prior to the nesting season at each site), and a GPS unit recorded the nest marker for identifying the precise nesting coordinates once the nesting season was over. To prevent data duplication and reduce disturbance, only the initial GPS location, species identification, and egg count were recorded. No repeated nest-level measurements were conducted in subsequent visits, and hatching success was not assessed, as reproductive outcomes were beyond the scope of this study. Importantly, all final nesting GPS coordinates used for analysis were collected after the conclusion of the nesting season to ensure zero disturbance to active nests.

4.1.2. Minimum distance to vegetation, roads, and buildings

To evaluate landscape-level habitat structure and potential anthropogenic influences, the minimum distance from each nesting location to the nearest vegetation line, roadway, and building was calculated using QGIS geospatial analysis tools (Figure 3). The orthophotography used in this study corresponds to the 2024 New York City orthoimagery dataset (New York State GIS Clearinghouse, 2024). All map data presented in the figures were projected using the NAD83/UTM Zone 18N coordinate reference system (EPSG:32618). These spatial metrics provided quantitative measures of habitat isolation, exposure, and proximity to infrastructure.

4.1.3. High tide measurement

To establish inundation baselines and evaluate potential exposure to tidal flooding, four high-tide measurements were collected throughout the season. GPS tracking was conducted by walking the highest visible water line during peak tidal events, typically associated with full moon cycles when tides are elevated. Among these measurements, the absolute highest GPS-registered tidal line across the season was selected for analysis, providing a conservative and ecologically meaningful estimate of regular inundation risk (Figure 4). This baseline allowed identification of nests potentially vulnerable to daily tidal encroachment or extreme weather events.

Figure 3. Vegetation, roads, and buildings lines at: a) Beach 37th St.-56th St., b) Fort Tilden, and c) Breezy Point Ocean Side and Bay Side.

4.1.4. Atmospheric variables measurements

To examine atmospheric drivers influencing nest initiation timing, atmospheric data were obtained from the Local Climatological Data (LCD) dataset provided by the National Oceanic and Atmospheric Administration (NOAA), through the National Centers for Environmental Information (NCEI). Specifically, records from the John F. Kennedy (JFK) International Airport weather station were used for the months of April through August 2025 (NOAA, 2026), as this station is geographically closest to the primary nesting sites at Fort Tilden and Rockaway Beach.

Daily summaries of key variables were extracted, including maximum and minimum air temperature, total precipitation, and average daily values of wind speed, relative humidity, and cloud cover. These variables were integrated into statistical analyses to evaluate their influence on nesting phenology. The dataset also allowed identification of extreme weather events, such as cold snaps or heavy precipitation episodes, and their potential effects on nest initiation. Prior to analysis, meteorological data underwent systematic cleaning and aggregation, where precipitation was represented as total daily liquid content, temperature variables corresponded to daily maximum and minimum values, and wind speed, relative

humidity, and cloud cover were calculated as daily averages from sub-daily observations, ensuring alignment between atmospheric conditions and the date of nest initiation recorded in the field. Because atmospheric data were obtained from a single weather station (JFK), these conditions were consistent across sites and differences among locations reflect variation in the timing of nest observations rather than spatial variation in weather.

Figure 4. High tide line at: a) Beach 37th St.- 56th St., b) Fort Tilden, c) Breezy Point Ocean Side, and d) Breezy Point Bay Side.

4.1.5. Beach slope measurement

To quantify local geomorphological conditions at each nesting site, beach slope was measured as an indicator of drainage capacity, tidal exposure, and habitat suitability. Using a rangefinder, the observer stood at the lowest tide line and projected a perpendicular line toward the higher beach profile to determine the horizontal distance and vertical elevation difference (Figure 5). The slope angle (θ) for each nest location was then calculated using the trigonometric relationship:

$$\theta = \tan^{-1}\frac{h}{R}$$

where h represents the elevation differential and R the horizontal distance measured by the rangefinder. This calculation provided a standardized quantitative measure of microhabitat topography for each nest.

Collectively, these measurements establish a multi-scale dataset linking fine-scale geomorphological conditions, landscape configuration, tidal risk, and atmospheric drivers to shorebird nesting patterns across the study area.

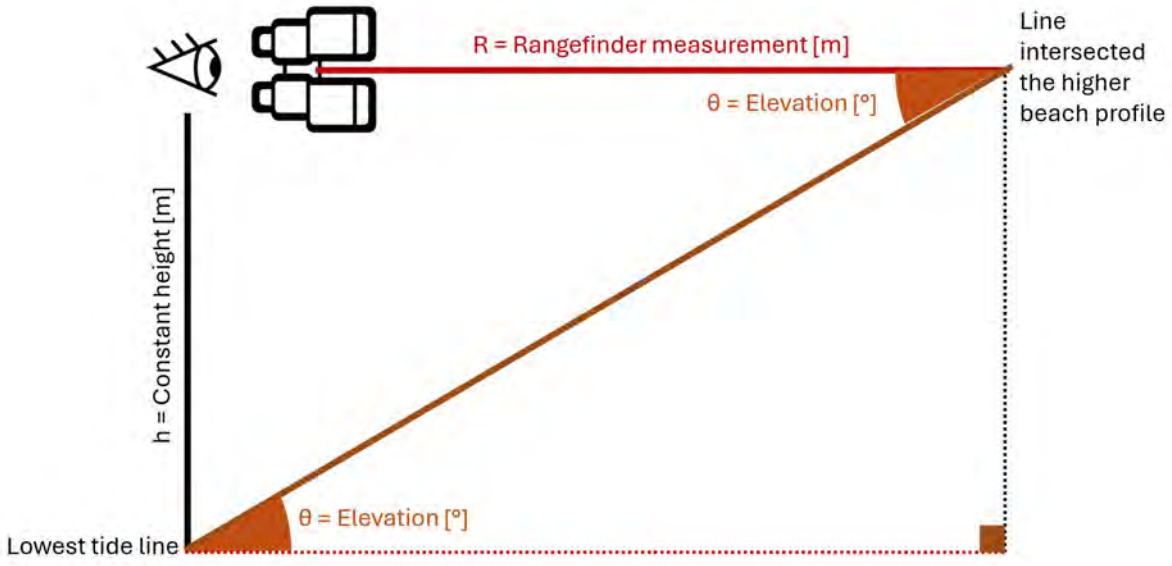

Figure 5. Conceptual diagram of beach slope measurement at nesting sites.

4.2. Data processing and statistical analysis

All spatial and statistical analyses were conducted using the Python programming language. Data processing and visualization were implemented using the libraries *pandas, numpy, matplotlib*, and *seaborn*, while statistical modeling was performed using *statsmodels, scipy, pyGAM*, and *scikit-learn*. Spatial calculations were conducted using *geopy* for geodesic distance estimation and *shapely* for geometric operations involving spatial features.

Nest locations were recorded using geographic coordinates (latitude and longitude). Distances among nests and between nests and environmental features (e.g., high tide line, vegetation, streets, and buildings) were calculated using geodesic distances based on the Haversine formulation, which estimates the great-circle distance between two points on the Earth's surface (Panigrahi, 2014). Pairwise nest distances were calculated using geodesic calculations implemented through the *geopy.distance* module, while distances between nests and spatial features represented by linear elements were calculated as the shortest distance between a point and a line using Point and LineString geometries from the *shapely.geometry* module.

Because the exact dates of clutch initiation and hatching were not available, the date of nest observation was used as a proxy for nest activity. Incubation periods for the focal species range from approximately three to four weeks: about 24-27 days for American Oystercatcher, 21-23 days for Common Tern, 19-25 days for Least Tern, and 26-28 days for Piping Plover (Arnold et al., 2020; Elliott-Smith & Haig, 2020; Thompson et al., 2020; Working Group et al., 2020). Based on these incubation durations and the weekly survey schedule, minimum interspecific nest distances were calculated using a temporal window of ±14 days around the observation date. This window approximates the typical period during which nests remain active while accounting for uncertainty in detection timing, thereby providing a biologically realistic estimate of contemporaneous spatial proximity among nests.

Exploratory linear models and diagnostic tests were conducted using *statsmodels* and *scipy*. GLMs with Poisson errors and robust standard errors were fitted using *statsmodels*, including additional models incorporating species and sites as categorical predictors. Exploratory GLMMs were implemented using the *statsmodels.genmod.bayes_mixed_glm* module. Potential nonlinear relationships were evaluated using GAMs implemented with the *pyGAM* library. Finally, a RF regression model was fitted using *scikit-learn*, and permutation importance was calculated using the *sklearn.inspection* module to assess the relative importance of predictors.

5. Results and Discussion

5.1. Descriptive Statistics

Descriptive statistical analyses were applied to the variables defined in the Data and Methods section to characterize patterns in shorebird nesting across the Rockaway Peninsula. This framework enables evaluation of how interactions among reproductive behavior, coastal geomorphology, local climate, and anthropogenic disturbance shape microhabitat selection, phenology, and reproductive investment. Four focal species were considered: American Oystercatcher (OC), Common Tern (CT), Least Tern (LT), and Piping Plover (PP). Nesting patterns were analyzed across four study sites: Beach 37th-56th Streets (B), Fort Tilden (FT), Breezy Point Ocean Side (OS), and Breezy Point Bay Side (BS). These abbreviations are used throughout the following sections.

A total of 121 nests were recorded across the study sites, with OC representing the majority (61 nests), followed by LT (35 nests), PP (15 nests), and CT (10 nests). Nest distribution varied among sites, with the highest number observed at B (65 nests), followed by OS (32 nests), FT (16 nests), and BS (8 nests). In terms of reproductive investment, a total of 269 eggs were documented. OC again accounted for the largest share (145 eggs), followed by LT (58 eggs), PP (51 eggs), and CT (15 eggs). Egg abundance was highest at B (127 eggs), followed by OS (76 eggs), FT (43 eggs), and BS (23 eggs).

5.1.1. Number of Eggs

Clutch size was analyzed across the four focal species and study sites to evaluate spatial variation and interspecific differences in reproductive strategy (Figure 6). The number of eggs per nest represents a key component of reproductive investment and reflects both environmental constraints and habitat quality, as it directly influences fecundity and population dynamics in shorebirds (Dinsmore, 2019).

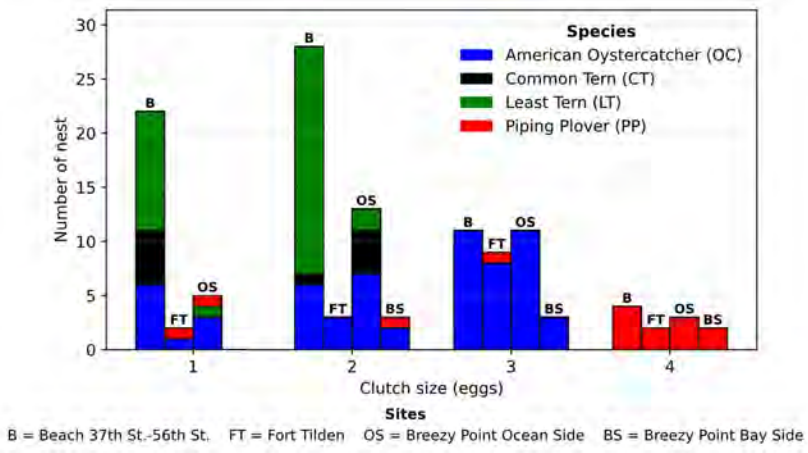

Figure 6. Number of eggs per nest by species and site.

OC exhibited predominantly two- and three-egg clutches across all sites, with a clear dominance of three-egg nests at B and OS. At FT and BS, sample sizes were smaller, but the same general pattern was observed, with few single-egg clutches. This distribution is consistent with a relatively stable reproductive strategy across sites, with minor variation potentially associated with local habitat conditions or breeder experience. Previous studies report clutch sizes of one to four eggs, with three eggs typically representing the modal value in Atlantic coast populations (Baker & Michael, 1980; Nol et al., 1984; Toland, 1999).

In contrast, CT showed a predominance of one- and two-egg clutches, particularly at B and OS. The presence of single-egg nests may reflect early laying stages, replacement attempts, or suboptimal conditions during initial reproduction. Similar patterns were observed at FT and BS, despite lower sample sizes, with relatively few three-egg clutches. In CT, clutch size is known to vary with environmental conditions and food availability, and reduced clutches are often associated with renesting or late-season breeding (Gochfeld, 1977; Wiggins et al., 1984).

LT displayed a clear dominance of two-egg clutches, especially at B, where nesting abundance was highest. Occasional single-egg nests, particularly at OS, may reflect early or failed reproductive attempts. The relative consistency of clutch size across sites suggests a stable reproductive strategy under varying environmental conditions. Previous studies indicate that variation in LT reproductive output is more strongly

influenced by habitat characteristics and colony dynamics than by large shifts in clutch size (Atwood & Massey, 1988; Baasch et al., 2017).

PP showed the most distinct pattern, with a strong predominance of four-egg clutches, particularly at B and OS. Four-egg clutches were also recorded at FT and BS, although less frequently, alongside some two- and three-egg nests. This pattern is consistent with the typical reproductive strategy of the species, as most PP clutches contain four eggs (Cairns, 1982; Cohen et al., 2009). Smaller clutches may result from incomplete laying or environmental disturbance. In some cases, PP have been observed relocating nests or eggs in response to habitat changes such as rising water levels, reflecting behavioral flexibility in protecting reproductive investment (Wiltermuth et al., 2009).

Across sites, B supported the highest number of nests and the widest range of clutch sizes across all species, suggesting favorable breeding conditions that allow both high nest density and substantial reproductive investment. In contrast, FT and BS showed smaller sample sizes and lower variability in clutch size, potentially reflecting spatial or environmental constraints. OS exhibited intermediate patterns, with clutch sizes comparable to B but lower overall abundance. In coastal shorebird systems, reproductive outcomes may also be influenced by social interactions; for example, plovers nesting near tern colonies may benefit from reduced predation risk due to collective defense (Powell, 2001).

Overall, the variation in the number of eggs per nest reinforces the idea that spatial differences on the Rockaway Peninsula influence not only nest distribution but also key aspects of reproductive investment. The relative consistency of clutch sizes within each species suggests stable reproductive strategies, while variations between zones may be associated with differences in habitat quality, availability of nesting space, and the degree of environmental or anthropogenic disturbance affecting breeding conditions (Cohen et al., 2009; Dinsmore, 2019).

Temporal dynamics of egg production and reproductive phenology relative to seasonal thermal conditions were analyzed using daily egg totals by species and site with maximum temperature (Figure 7).

Reproductive activity was concentrated between early May and mid-July, coinciding with a progressive increase in maximum temperature. Peak egg-laying occurred under intermediate temperatures (approximately 18-28°C), while activity declined markedly above 30°C, indicating a synchronization of breeding onset with favorable thermal conditions. Ground-nesting shorebirds are particularly sensitive to temperature because eggs develop in exposed substrates where thermal conditions directly influence incubation behavior (Andes et al., 2020). Similar temperature-driven shifts in breeding phenology have been documented in multiple shorebird species (Kwon et al., 2018; Abernathy et al., 2023). More broadly, the timing of seabird breeding cycles is often closely linked to seasonal environmental conditions such as

temperature, food availability, and other climatic factors that influence reproductive decisions and nesting success (Schreiber & Burger, 2001).

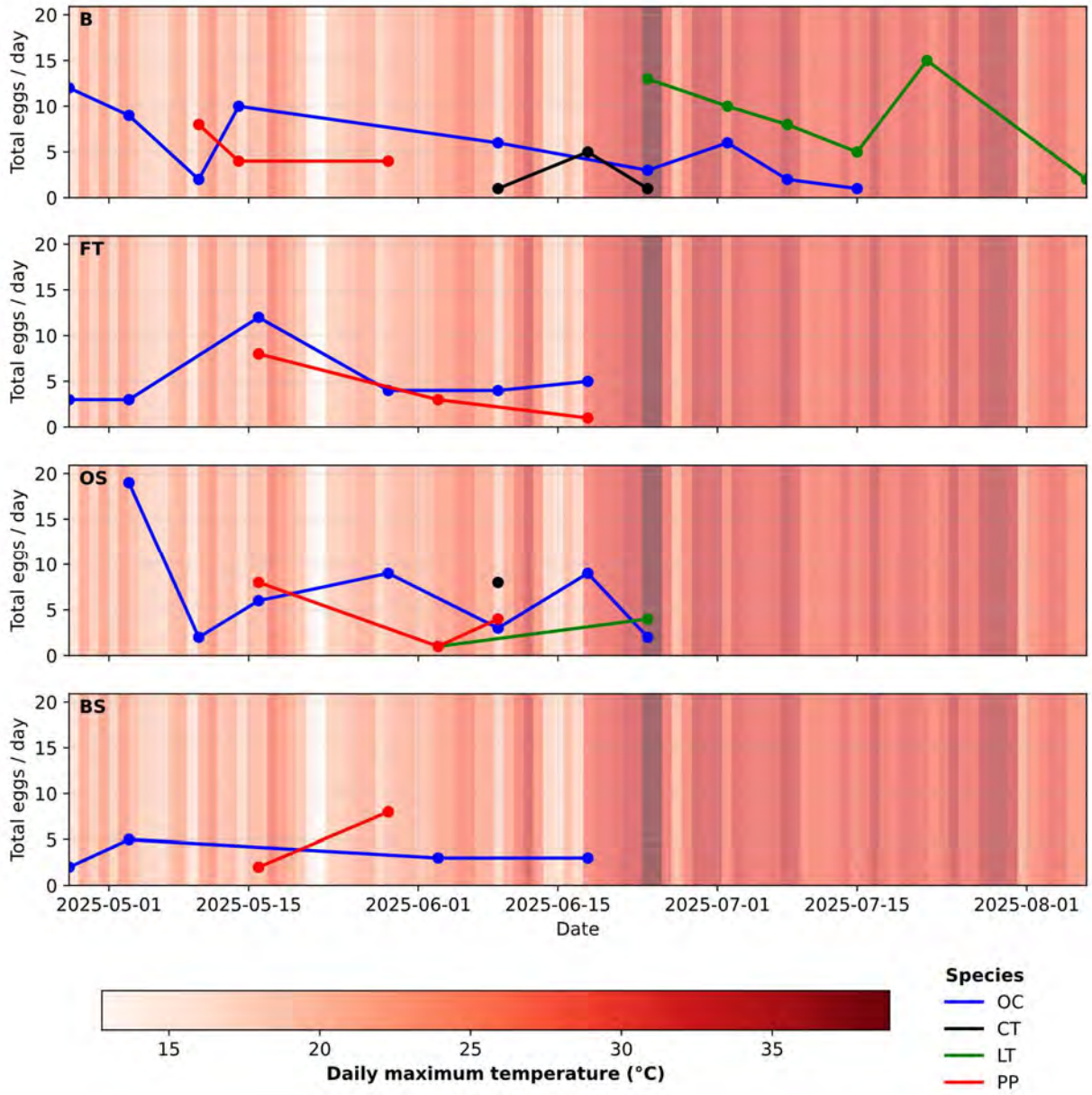

Figure 7. Daily total number of eggs by species and site, with maximum daily temperature.

The highest intensity and duration of breeding activity were observed at B. OC showed sustained egg-laying from early May, followed by a gradual decline toward mid-June. CT and PP exhibited shorter and more temporally restricted peaks, whereas LT showed delayed peaks between late June and mid-July. This staggered pattern suggests temporal partitioning among species, potentially reducing competition for nesting space and resources. In seabird communities, breeding cycles are often synchronized within species but differ among coexisting species, allowing shared habitat use with reduced temporal overlap (Schreiber

& Burger, 2001). Despite the progressive increase in maximum temperature, reproductive activity persisted in this site for an extended period, indicating habitat conditions that buffer against heat stress. Habitat characteristics such as substrate composition, elevation, and access to foraging areas can moderate the effects of temperature on reproductive activity and nest success in coastal shorebirds (Farrell et al., 2018).

At FT, reproductive activity was shorter and less intense. OC displayed a clear peak in mid-May, followed by a decline, while PP showed a brief reproductive window ending in early June. The absence of nesting during periods of higher temperatures suggests greater sensitivity to thermal conditions or spatial constraints limiting sustained reproduction. Elevated temperatures can impose physiological and behavioral trade-offs between thermoregulation, incubation, and foraging (van de Ven et al., 2019).

Meanwhile, OS exhibited high temporal variability in egg production, particularly for OC, with early peaks and fluctuations throughout May and June. CT and PP showed isolated peaks, while LT exhibited later and less intense activity. This variability may reflect environmental instability or a higher frequency of nest failure and renesting, a common strategy in shorebirds despite reduced success in later attempts (Claassen et al., 2014). Finally, BS showed the lowest reproductive intensity and duration, with egg-laying limited to a few events during May and early June. The absence of activity during warmer periods suggests that this site provides less favorable conditions for sustained breeding, possibly due to habitat constraints, disturbance, or reduced buffering against heat stress.

In sum, the time series shows that shorebird breeding on the Rockaway Peninsula is closely linked to the seasonal thermal cycle. Weather variability and seasonal climatic patterns are widely recognized as important drivers of seabird breeding timing, reproductive success, and population dynamics through both direct physiological effects and indirect influences on habitat conditions and food availability (Schreiber & Burger, 2001; Stutzman & Fontaine, 2015; Suthar et al., 2025). Differences between sites indicate that habitat quality and configuration modulate the birds' ability to sustain breeding over time, highlighting B as the main breeding site and the other sites as more limiting environments in phenological and thermal terms. Spatial differences in reproductive success and nesting persistence among breeding areas are commonly associated with local habitat conditions, disturbance regimes, and weather variability (McGuire et al., 2020; Guild et al., 2024).

5.1.2. Nest distances among species

The spatial structure of nests was evaluated using the minimum distances between conspecific nests and between nests of different species (Figure 8). These metrics allow assessment of local patterns of aggregation, dispersion, and territorial spacing. Nest spacing is a key component of shorebird breeding

ecology because territorial behavior, habitat selection, and social interactions influence how individuals are distributed across nesting habitats (Maslo et al., 2016).

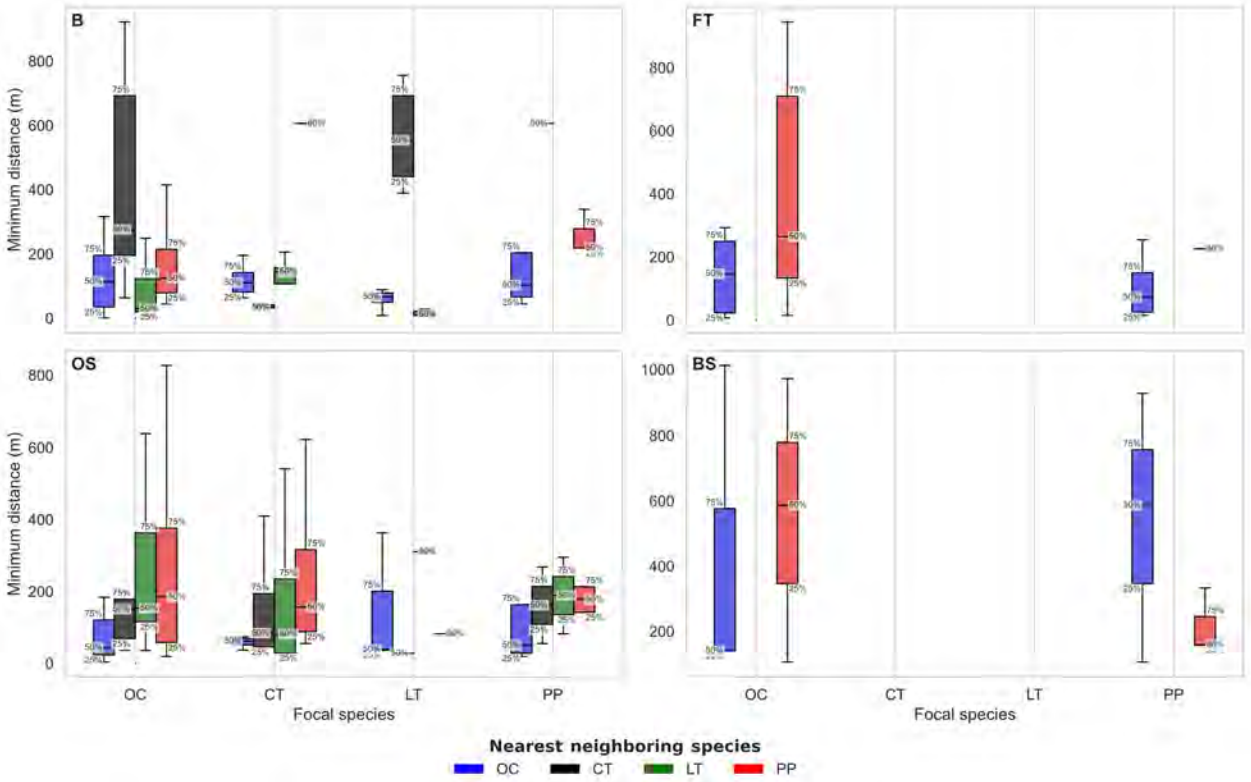

Figure 8. Minimum intra- and interspecific nest distances by species and site.

OC showed moderate spatial aggregation in sites where the species was more abundant, particularly at B and OS, where distances between conspecific nests generally remained below approximately 150-200 m, indicating a tolerance of relatively close nesting neighbors. Distances between OC and other species varied among sites. At B, OC nests were often located far from CT colonies, suggesting spatial separation from densely aggregated colonial breeders. By contrast, distances between OC and LT or PP were generally more moderate, suggesting partial spatial overlap within the nesting habitat. OC is known to show flexibility in nest-site selection across coastal environments, often using sandy or wrack substrates that reduce flooding risk and support successful breeding (Lauro & Burger, 1989). At FT and BS, where only OC and PP were present, distances between these species were highly variable. This pattern is consistent with a more dispersed distribution associated with lower nest densities.

CT showed consistently very short conspecific distances at both B and OS, reflecting the species' strongly colonial nesting strategy and resulting in compact colonies. Colonial nesting in terns produces very short nearest-neighbor distances due to dense aggregation and collective predator defense (Burger & Lesser, 1978; Burger & Gochfeld, 1988). Distances between CT and other species were generally larger than intra-

colony distances, suggesting that CT colonies occupied relatively discrete sectors of the beach. This pattern reflects strong within-species aggregation and limited spatial overlap with other breeders at fine scales.

LT displayed a similar pattern, with very short distances between conspecific nests at B, indicating strong colonial clustering, whereas OS distances were more variable and tended to be larger, indicating a less compact colony structure. However, distances between LT and other species were generally moderate rather than extremely large, suggesting partial spatial overlap with other shorebirds. Nest clustering in tern colonies is often shaped by habitat structure and the availability of suitable nesting substrates, which can concentrate nests within relatively small areas of otherwise extensive beach habitat (Burger & Gochfeld, 1988). This arrangement indicates fine-scale spatial partitioning within shared nesting habitat.

PP nests showed relatively consistent spacing across all sites, with most conspecific distances falling within a similar range of approximately 200-400 m. This pattern is consistent with the territorial breeding behavior typical of the species. Although spacing occurred within a similar range across sites, variation within this range differed slightly, with FT and BS tending toward larger distances and B and OS showing somewhat more clustered distributions. Territorial interactions and aggressive behavior toward nearby individuals often generate regular spacing patterns among plover nests across suitable beach habitat (Bergstrom & Terwilliger, 1987). Distances between PP and other species were usually intermediate, indicating that PP can occupy the same general nesting sites as other shorebirds while maintaining spatial separation from nearby nests. In several coastal systems, PP have been observed nesting near tern colonies, where proximity to colonial species may provide antipredator benefits without eliminating individual territorial spacing (Burger, 1987).

Clear differences in spatial structure were observed among study sites. B, where all four species were present, showed the most complex configuration, with dense CT and LT colonies coexisting with more dispersed OC and PP nests, suggesting that tern colonies occupied distinct sectors of the beach. FT, where only OC and PP nested, exhibited a simpler but highly variable pattern, with distances ranging from short to relatively large, suggesting use of separate areas within the beach system. OS also supported all four species but showed a more interspersed arrangement, in which colonial clustering of terns persisted while interspecific distances remained moderate, indicating greater spatial coexistence. In contrast, BS showed the most dispersed nesting pattern, with only OC and PP present and relatively large distances both within and between species, consistent with lower nest densities and broader spacing of nesting territories.

Nest spacing across the study system reflected both species-specific reproductive strategies and local habitat configuration. Colonial breeders (CT and LT) formed tightly clustered groups with minimal conspecific distances, whereas PP maintained broader spacing consistent with territorial nesting behavior.

OC showed an intermediate pattern, with moderate clustering but greater variability in spacing. Spatial patterns also varied among beaches, indicating that local environmental conditions influenced nest distribution. Beaches supporting multiple species showed more complex arrangements, with clustering and spatial segregation occurring simultaneously, whereas beaches with fewer species tended to show more dispersed nesting patterns. These results indicate that both reproductive strategy and habitat configuration shape the spatial structure of shorebird nesting communities within the Rockaway Peninsula. At broader spatial scales, variation in habitat overlaps among beach-nesting birds may reflect differences in ecological niches and breeding strategies, with some species acting as indicators of suitable habitat for others (Maslo et al., 2016; Forsberg, 2024).

5.1.3. Distance to the high tide line and vegetation

Minimum distances from nests to two structural components of the coastal habitat, the high tide line and the vegetation limit, were analyzed to evaluate spatial selection patterns across the four study sites (Figure 9). These metrics provide insight into trade-offs among flood risk, open substrate availability, and protection from disturbance or predation. Habitat selection in beach-nesting shorebirds is strongly influenced by geomorphological features such as beach width, elevation, and distance to shoreline or vegetation, which determine both nesting suitability and exposure to environmental risks (Farnsworth et al., 2018; Zeigler et al., 2021).

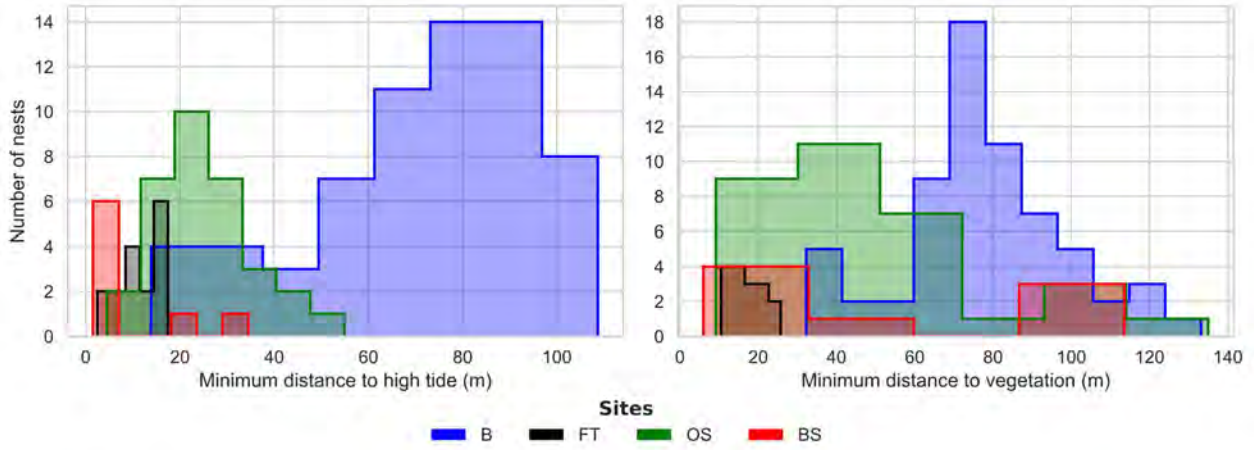

Figure 9. Minimum distance from nests to the high tide line and vegetation by site.

Distance to the high tide line differed clearly among study sites. At B, nests were predominantly located at relatively large distances, concentrated between approximately 50 and 100 m from the high tide line. This pattern indicates selection of areas less susceptible to flooding, likely associated with greater substrate stability and lower risk of nest loss during tidal events or storms. Coastal waterbirds are particularly vulnerable to flooding during the breeding season because nests are typically located on low coastal substrates exposed to tidal fluctuations and storm-driven overwash (Erwin et al., 2006). Increasing sea levels

and the greater frequency of extreme weather events predicted under climate change scenarios may further increase flooding risk in coastal breeding habitats (van de Pol et al., 2024).

By contrast, nests at FT and OS were generally much closer to the high tide line, with most located between 10 and 40 m away, indicating greater use of the upper intertidal zone. At BS, although the number of nests was lower, most were located very close to high tide, generally less than 20 m away, suggesting strong spatial restriction of available habitat. Variation in nest placement relative to tidal zones has been documented in several coastal shorebird systems and may reflect local geomorphological constraints that limit the availability of suitable nesting substrate on barrier beaches (Walker et al., 2019; Zeigler et al., 2019).

Distance to vegetation also varied markedly among study sites. At B, nests were mostly located at intermediate to long distances from vegetation, with a clear peak between 60 and 100 m, consistent with a preference for open beach areas that may reduce predation risk and improve visibility. Many beach-nesting birds preferentially select open substrates with sparse or absent vegetation because these conditions reduce concealment opportunities for predators and allow adults to detect threats more effectively (Mazzocchi & Forys, 2005; Schulte & Simons, 2015).

At FT, distances to vegetation were generally short, with many nests located less than 30 m away, suggesting closer use of the beach-vegetation ecotone, possibly due to a narrower beach configuration or greater availability of shelter. Nest placement near dune vegetation has been observed in several coastal shorebird systems, where dunes can provide partial shelter from wind and disturbance while maintaining access to open nesting substrate (Walker, 2020).

At OS, nests showed a wider distribution of distances to vegetation, ranging from approximately 20 m to more than 120 m. This variability indicates greater habitat heterogeneity and suggests use of multiple breeding microenvironments, from open beach areas to sites closer to vegetation. Shorebirds frequently respond to spatial heterogeneity in coastal landscapes by exploiting multiple microhabitats depending on substrate availability, vegetation structure, and proximity to foraging areas (Garvey et al., 2013). At BS, despite the smaller number of nests, the distribution appeared bimodal, with some nests very close to vegetation and others much farther away, likely reflecting the limited availability of continuous sandy substrate in this site.

Considered jointly, both metrics reveal a clear gradient in habitat selection among study sites. B was characterized by nests located far from both high tide and vegetation, suggesting the availability of a wide and relatively stable beach. In contrast, FT, OS, and especially BS appeared to impose stronger spatial constraints, forcing birds to nest closer to the high tide line or vegetation. Human disturbance and coastal

development can further reduce the availability of suitable nesting habitat on barrier islands, increasing the likelihood that birds use suboptimal nesting locations (Virzi et al., 2016).

Distances to the high tide line and vegetation indicate that nest-site selection was not random but closely related to the physical configuration of the coastal habitat. Nest placement in beach-nesting shorebirds reflects trade-offs among flooding risk, predator exposure, and habitat structure, all of which can influence reproductive success and population dynamics (Schulte, 2012; Call, 2025). Differences among study sites likely reflect variation in available space and local geomorphological conditions, helping to explain broader patterns in nest density and spatial distribution across the Rockaway Peninsula. In particular, the relatively narrow beach width at FT likely constrained available nesting habitat, resulting in nests being placed closer to both the high tide line and vegetation compared to wider sites such as B and OS.

5.1.4. Distance to roads and buildings

Minimum distances from nests to two components of human infrastructure, roads and buildings, were analyzed to assess patterns of avoidance or tolerance of anthropogenic disturbance across the four study sites (Figure 10). These metrics provide insight into the influence of urbanization and human access on nest-site selection. Urbanization and road infrastructure can affect bird distribution and habitat use by modifying landscape structure and increasing human disturbance, often leading sensitive species to avoid highly disturbed sites (Palomino & Carrascal, 2007; Graells et al., 2022).

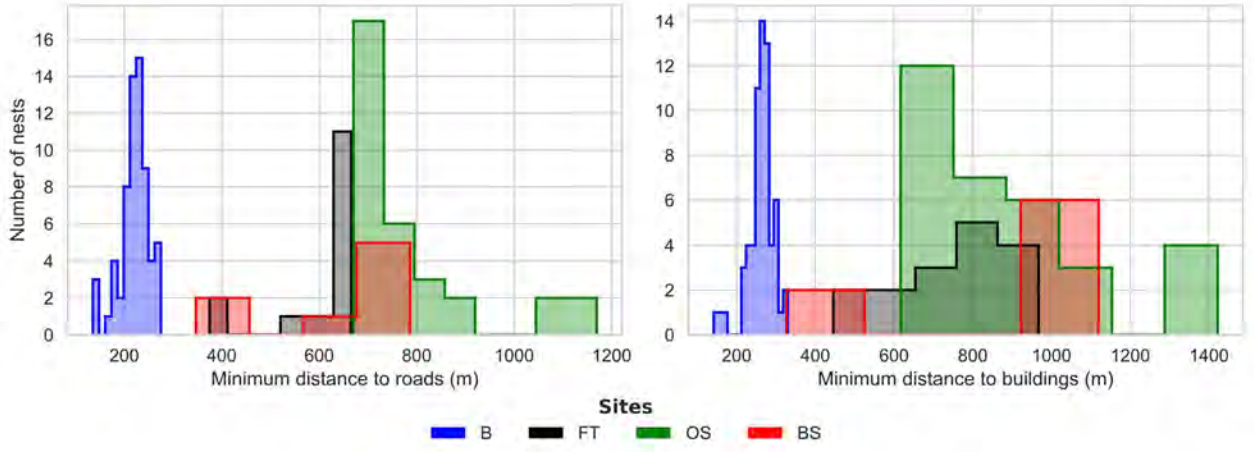

Figure 10. Minimum distance from nests to roads and buildings by site.

Distance to roads showed strong contrasts among study sites. At B, nests were located relatively close to roads, concentrated mainly between approximately 150 and 250 m, suggesting a relatively high tolerance of nearby road infrastructure under intense urban pressure and limited availability of continuous natural habitat. Roads can affect bird distributions over considerable distances by increasing noise, disturbance, and predator access, thereby reducing habitat suitability for some species (van der Zande et al., 1980; Forman

et al., 2002). At FT, distances to roads were considerably greater, with most nests located between 600 and 700 m, indicating less direct influence from vehicular traffic and a lower level of human disturbance. Lower anthropogenic disturbance is often associated with higher probabilities of nesting occurrence in beach-nesting birds sensitive to human presence (Virzi, 2010). At OS, nests occurred at intermediate to large distances from roads, ranging from approximately 650 m to more than 1000 m, suggesting the availability of extensive beach areas relatively far from road access. Human presence near breeding areas can alter incubation behavior and reduce reproductive success in coastal birds when disturbances are frequent (Borneman et al., 2016). At BS, although the number of nests was lower, distances to roads generally ranged from 350 to almost 800 m, reflecting spatial restriction by surrounding infrastructure.

Distance to buildings showed a similar spatial gradient, although values were generally larger. At B, nests were mostly located between 200 m and 300 m from buildings, indicating that birds used breeding habitat relatively close to permanent urban structures. Some coastal bird species can show behavioral flexibility and persist in modified environments when suitable nesting substrate remains available within urban landscapes (Forys & Borboen-Abrams, 2006). At FT, distances to buildings were greater, concentrated between approximately 700 and 900 m, consistent with lower building density and a more natural landscape context. At OS, distances varied widely, ranging from about 600 m to more than 1400 m, indicating strong spatial heterogeneity and the presence of extensive areas free of infrastructure. Maintaining sufficient spatial buffers between nesting birds and disturbance sources can reduce behavioral disruption and improve breeding success in colonial seabirds (Rodgers Jr. & Smith, 1995; Althouse et al., 2019). At BS, distances to buildings ranged from moderate to long, generally between 400 and 1100 m, although the smaller number of observations again suggests spatial constraints in this site.

These results reveal a clear gradient of anthropogenic influence among study sites. B was characterized by the highest proximity of nests to both roads and buildings, indicating either tolerance of, or forced coexistence with, urban infrastructure. In contrast, FT and OS showed greater distances to infrastructure, reflecting more natural conditions and lower levels of direct human disturbance. BS occupied an intermediate position, with patterns suggesting a combination of habitat limitation and anthropogenic pressure. The distribution of nests in urbanized coastal landscapes often reflects a balance between habitat availability and tolerance of human disturbance in heavily modified barrier island systems (Graells et al., 2022). Minimum distances to roads and buildings indicate that nest-site selection was strongly influenced by the presence of human infrastructure. Coastal development can also limit the formation and persistence of early successional habitats that are essential for many beach-nesting birds, further affecting where breeding pairs establish nests (Zeigler et al., 2019). Differences among study sites suggest that access to

areas farther from anthropogenic disturbance may be an important factor underlying variation in nest density and distribution across the Rockaway Peninsula.

Overall, nest distribution across the Rockaway Peninsula reflected the combined influence of species-specific nesting strategies, local habitat configuration, and anthropogenic disturbance. Distances among nests revealed contrasting reproductive behaviors, with colonial species forming dense clusters and territorial species maintaining broader spacing. At the same time, nest placement relative to the high tide line and vegetation suggests that birds balance flooding risk, predator exposure, and habitat availability when selecting breeding sites. Distances to roads and buildings further highlight the role of human infrastructure in shaping nest distribution, with some areas allowing greater separation from urban disturbance than others. Together, these patterns indicate that natural habitat characteristics and human landscape modification interact to determine where shorebirds establish nests, ultimately influencing local nest density and the spatial organization of the breeding community.

5.1.5. Atmospheric conditions

Atmospheric conditions recorded on the day of nesting were analyzed for each nest (Figure 11). These variables characterize the immediate climatic context of nest initiation and allow comparison among study sites within the Rockaway Peninsula. Weather conditions can influence multiple aspects of shorebird breeding ecology, including nest initiation, reproductive timing, and nest success, particularly in species that nest in exposed coastal environments (Schreiber & Burger, 2001; Weiser et al., 2018). Atmospheric conditions were assigned based on the date of nest observation, used here as a proxy for nest activity (see Data and Methods section).

Wind speed showed a concentration of low to moderate values across all study sites. Most nests were established under wind speeds below 20 km/h, with a marked peak between approximately 10 and 15 km/h. B exhibited the widest range, including some nesting events associated with stronger winds exceeding 30 km/h, whereas FT, OS, and BS showed narrower distributions with few extreme values. This distribution suggests that nesting generally occurred under relatively stable wind conditions, although birds in more exposed or urbanized areas may tolerate greater variability. Wind conditions can influence shorebird activity patterns and population dynamics because strong winds affect foraging efficiency, flight costs, and nest exposure in open habitats (Suthar et al., 2025).

Relative humidity was regularly high across sites, with most values between 70% and 95%. At B, the distribution was broader, with peaks at both intermediate values (around 60%) and high values (>85%), whereas nesting was concentrated under high humidity conditions at FT and OS. BS showed predominantly high humidity values, although the sample size was smaller. These results indicate that nesting frequently

occurred under humid atmospheric conditions typical of coastal environments, consistent with the adaptation of many shorebird species to marine-influenced climatic regimes (Schreiber & Burger, 2001).

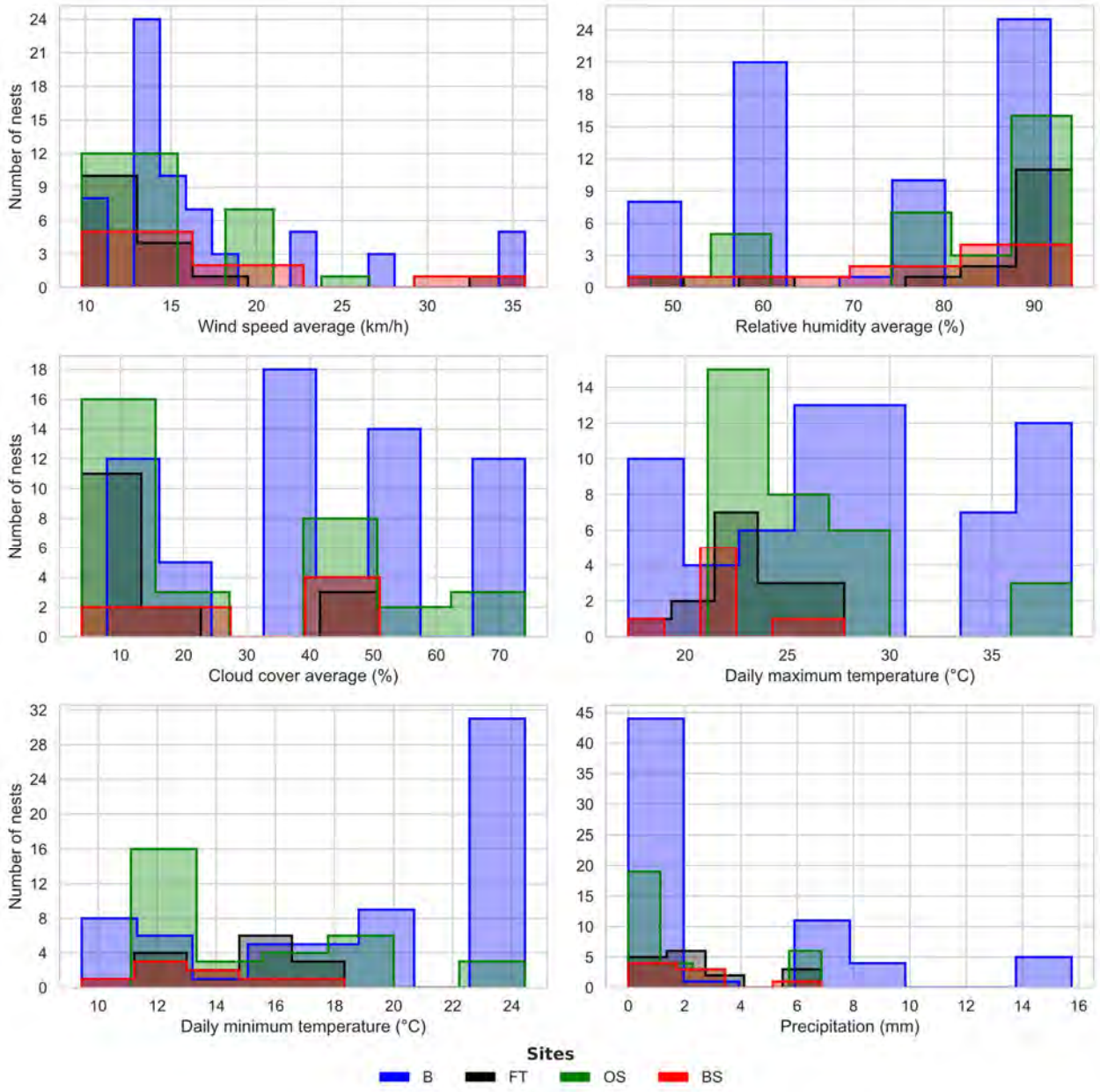

Figure 11. Atmospheric conditions by site.

Cloud cover showed a bimodal distribution in several study sites. At B, nests occurred under both low (<20%) and intermediate to high (40-70%) cloud cover. FT and OS showed a higher frequency of nesting under low to moderate cloud cover, whereas BS included relatively few observations, mainly at intermediate levels. This pattern indicates that nest initiation was not restricted to clear conditions and could occur under a broad range of cloud cover values. Ground-nesting birds in open habitats often experience substantial

daily weather variability during the breeding season, and reproductive activity may occur across a wide range of atmospheric conditions (Clements et al., 2022).

Maximum temperature on nesting days was concentrated mainly between 20°C and 35°C. B again showed the widest range, including values close to 37-38°C, whereas FT and OS showed narrower distributions, generally between 22°C and 30°C. BS was mostly characterized by intermediate values. This pattern suggests that nesting occurred predominantly under warm, but not extreme, thermal conditions, with some tolerance of high maximum temperatures in more environmentally heterogeneous areas. Temperature is an important component of shorebird reproductive ecology because high thermal conditions can influence nest attendance behavior and thermoregulation in incubating adults (Andes et al., 2020).

Minimum temperature was relatively consistent across study sites, with most values concentrated between approximately 10°C and 18°C. B showed some higher values, close to 22-24°C, which may reflect urban heat island effects or local atmospheric conditions. In general, nesting appeared to occur when nighttime or early morning temperatures were moderate, rather than under very cold conditions. Temperature during the early breeding season can influence clutch initiation timing and other reproductive traits in shorebirds (Kwon et al., 2018).

Precipitation was minimal or absent in most cases. The vast majority of nests were established on days with no recorded rainfall or very low precipitation (<2.5 mm). Only B included a few nesting events associated with moderate rainfall, and these were infrequent. This pattern suggests that birds generally initiated nesting on dry days, likely reducing the risks of egg cooling, nest flooding, and substrate compaction. Rainfall can negatively affect ground nests by increasing the probability of flooding or nest failure, particularly in exposed coastal habitats (Krogh & Schweitzer, 1999; Guild et al., 2024).

In summary, atmospheric conditions on nesting days indicate that breeding began under a relatively narrow set of climatic conditions characterized by low to moderate winds, high humidity, warm temperatures, and little or no precipitation. Although the range of values differed among study sites, especially at B, the overall pattern suggests that nest initiation was not random with respect to weather, but tended to occur under relatively stable and favorable coastal conditions. Weather variability can influence multiple stages of the annual cycle of migratory shorebirds, affecting breeding decisions, reproductive success, and ultimately population dynamics (Stutzman & Fontaine, 2015; Farrell et al., 2018).

5.1.6. Elevation

The elevation of nesting sites across the four study sites was analyzed to evaluate variation in vertical habitat selection (Figure 12). Elevation is a key component of microhabitat because it directly influences exposure to tidal flooding, storm events, and substrate stability. In coastal systems, even small differences in elevation

can strongly affect nest survival by determining exposure to overwash and flooding (Erwin et al., 2006; van de Pol et al., 2024). More broadly, birds may respond to environmental change through spatial shifts, including along elevational gradients, although such responses often occur more slowly than phenological adjustments (Neate-Clegg et al., 2024).

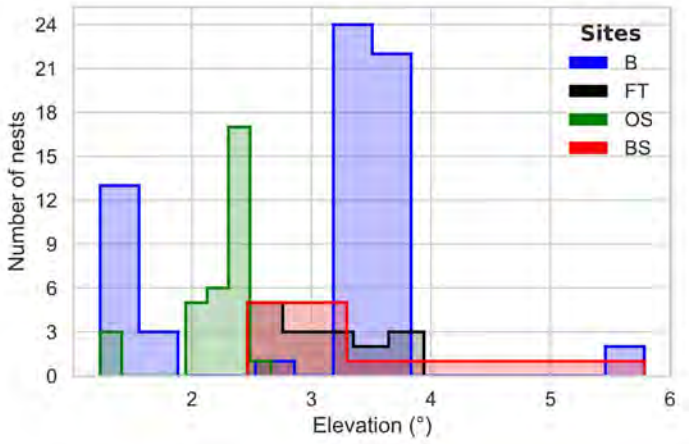

Figure 12. Elevation by site.

B exhibited the widest elevational range. Most nests were concentrated at intermediate elevations (approximately 2.5-4.0°), with a peak around 3.0-3.5°, although nests also occurred at lower values (around 1.5°) and at higher elevations (>5.5°). This distribution indicates broad availability of suitable habitat, allowing selection of relatively safe nesting sites while also reflecting occasional use of suboptimal elevations under high nesting density. Similar patterns have been reported in other beach-nesting shorebirds, where elevation and beach morphology strongly influence nest placement and flooding risk (Ruiz de Alegría-Arzaburu et al., 2025).

At FT, nests were restricted to a narrower elevational range, primarily between 2.8° and 4.0°. This concentration suggests consistent selection of elevated sites, likely associated with lower spatial pressure and more homogeneous topography. The absence of nests at very low elevations indicates avoidance of areas with higher flooding risk. Shorebirds frequently select nesting sites above typical high tide levels to reduce the probability of overwash events that can cause nest failure (Mazzocchi & Forys, 2005).

At OS, most nests occurred at relatively lower elevations (2.0-3.0°), indicating use of lower sections of the beach profile, possibly related to reduced topographic relief or proximity to the high tide line. Limited availability of higher ground in this site may increase vulnerability to flooding during storms or extreme tides, which are major drivers of nest failure in coastal systems (Sterling, 2017). At BS, despite the smaller sample size, elevations showed high variability, including both intermediate and high values (close to 5.5-6.0°). This pattern suggests opportunistic use of elevated microhabitats within a spatially constrained

environment, where suitable sites are limited. At fine spatial scales, shorebirds may respond to subtle topographic variation to reduce flooding risk and improve predator detection (Korne et al., 2020).

Overall, nesting elevation varied consistently among study sites and reflected both geomorphological availability and spatial constraints. In many coastal systems, the availability of suitable nesting habitat is strongly influenced by geomorphology, shoreline dynamics, and hydrological variability (Anteau et al., 2014; Zeigler et al., 2021). Wider and more stable beaches (B and FT) allowed clearer selection of intermediate to high elevations, whereas limited topographic variation appeared to restrict nest placement at OS and BS. These patterns highlight elevation as a central factor in nesting-site selection and exposure to flooding risk in coastal systems. As sea-level rise and increasing storm intensity continue to modify coastal topography, flooding risk in barrier island habitats is expected to increase (Lostritto & Taylor, 2015). Under these changing conditions, some bird species may attempt to track suitable environmental conditions through spatial shifts, including movement toward higher elevations, although phenological adjustments may occur more rapidly than geographic redistribution (Neate-Clegg et al., 2024).

In sum, nesting patterns across the Rockaway Peninsula reflect the combined influence of geomorphology, species-specific reproductive strategies, atmospheric conditions, and anthropogenic disturbance. Variation in clutch size and nesting density reflects differences in breeding behavior and spatial requirements among species, with colonial nesters forming clustered nesting areas while more territorial species maintain greater separation between nests. At the same time, nest placement relative to vegetation, the high tide line, and local elevation suggests that birds balance the need for protection from flooding and storms with the availability of open substrates suitable for nesting and chick mobility. Distances to roads and buildings further highlight the role of human infrastructure in structuring the spatial distribution of nests, with birds occupying areas that provide some degree of separation from direct anthropogenic disturbance. In addition, atmospheric conditions indicate that breeding tends to occur under relatively stable climatic conditions characterized by moderate temperatures, low to moderate winds, and minimal precipitation. Together, these patterns demonstrate that nesting site selection in this coastal system emerges from the combined influence of geomorphology, microhabitat availability, weather conditions, and human disturbance, emphasizing the complexity of habitat requirements for beach-nesting shorebirds in highly dynamic and urbanized barrier island environments.

5.2. Regression Modeling

5.2.1. Exploratory regression analysis

To explore the relationships between drivers and egg abundance, an exploratory MLR analysis was initially conducted using the number of eggs per nest as the response variable and a set of environmental,

atmospheric, and spatial variables as predictors. The initial set of explanatory variables included precipitation, wind speed, relative humidity, cloud cover, maximum and minimum temperature, elevation, distance to the high tide line, distance to vegetation, and distances to nearby streets and buildings. Prior to model fitting, the dataset was cleaned by removing observations with missing values in the explanatory variables. Some variables, particularly minimum distances between nests and certain species, contained empty values because those species were not present at specific sites. These missing values reflected ecological absence rather than incomplete measurements, preventing the definition of meaningful distances. Including these values would have prevented proper model fitting and potentially introduced bias. Therefore, such observations were excluded to ensure ecological consistency and statistical validity.

To evaluate the stability of the model and the influence of multicollinearity among predictors, three successive regression models were fitted (Table 1). Across these tests, the coefficient of determination remained relatively stable (R^2 ranging from 0.375 to 0.368), indicating that the removal of redundant predictors did not substantially reduce explanatory power. At the same time, the AIC decreased from 288.6 to 279.9, suggesting improved parsimony as unnecessary predictors were removed. Diagnostic tests showed consistent behavior across all specifications. The Shapiro-Wilk test produced p-values greater than 0.05, indicating no departure from residual normality. The Breusch-Pagan test also yielded p-values above 0.05, suggesting homoscedasticity. The Durbin-Watson statistic remained within the acceptable range (1.58-1.60), indicating no evidence of autocorrelation. Collectively, these diagnostics indicate that the models satisfied the main assumptions required for OLS estimation.

Differences among specifications were primarily driven by multicollinearity among predictors. In the initial specification (Test 1), minimum distances to roads and buildings exhibited extremely high variance inflation factors (VIF > 20), indicating severe collinearity with other spatial variables. Because these predictors represented anthropogenic features not consistently present across all sites and produced unstable estimates, both distance to roads and distance to buildings were removed (Test 2). Although this adjustment reduced extreme collinearity, several climatic predictors still showed elevated VIF values. A second stage of selection was therefore conducted to improve interpretability and reduce redundancy. Maximum and minimum temperature were strongly correlated; maximum temperature was retained due to its statistical significance and greater ecological relevance (e.g., heat stress and egg desiccation), while minimum temperature was removed. Similarly, cloud cover was retained over relative humidity because it more directly represents solar radiation attenuation at nesting sites. Wind speed was excluded due to its contribution to collinearity and lack of statistical significance. Precipitation was retained despite not being significant, given its low collinearity and ecological relevance.

Because both distance to the high tide line and distance to vegetation are influenced by beach width and coastal morphology, some degree of spatial correlation between these variables is expected. However, VIF values remained low, indicating that this relationship did not introduce problematic multicollinearity and allowing both predictors to be retained for ecological interpretation.

Table 1. Model fit statistics, diagnostic tests, and variance inflation factors (VIF) for the three regression specifications.

Criterion	Test 1	Test 2	Test 3
R^2	0.375	0.374	0.368
AIC	288.6	284.9	279.9
Shapiro-Wilk test p	0.531	0.664	0.580
Breusch-Pagan test p	0.190	0.178	0.277
Durbin-Watson statistic	1.595	1.584	1.581
VIF			
Minimum distance to vegetation	1.270	1.190	1.180
Minimum distance to high tide	2.930	2.252	1.660
Minimum distance to roads	**24.050**	-	-
Minimum distance to buildings	**20.907**	-	-
Wind speed	5.418	**5.254**	-
Relative humidity	6.830	**6.603**	-
Cloud cover	6.892	6.625	2.335
Maximum temperature	7.883	7.790	1.619
Minimum temperature	8.698	**8.286**	-
Precipitation	2.235	2.232	1.572
Elevation	1.244	1.118	1.074

The final specification (Test 3; Table 2) retained six predictors: precipitation, cloud cover, maximum temperature, elevation, distance to the high tide line, and distance to vegetation. This model explained approximately 36.8% of the variation in egg abundance. Maximum temperature showed a strong negative effect ($\beta = -0.074 \pm 0.014$, $p < 0.001$), indicating that higher temperatures were associated with lower egg counts. Elevation showed a statistically significant positive effect ($\beta = 0.178 \pm 0.076$, $p = 0.022$), suggesting that nests located at higher elevations tended to contain more eggs. Precipitation and distance to the high tide line showed marginal negative effects ($p \approx 0.10$), while cloud cover and distance to vegetation were not statistically significant.

Table 2. Parameter estimates (β), standard errors, and p-values for the final regression model (Test 3).

	β	std err	p
Constant	3.997	0.368	<0.001
Minimum distance to vegetation	0.001	0.002	0.681
Minimum distance to high tide	-0.004	0.003	0.099
Cloud cover	-0.002	0.005	0.583
Maximum temperature	-0.073	0.014	<0.001
Precipitation	-0.035	0.022	0.100
Elevation	0.177	0.076	0.022

Although diagnostic tests indicated that model assumptions were not violated, this stage should be interpreted as exploratory. In addition to providing an initial assessment of relationships, the MLR framework allowed identification of a subset of ecologically meaningful predictors. However, because the response variable represents discrete counts, linear regression does not fully capture its statistical properties. Therefore, these models were primarily used to guide variable selection for subsequent analyses based on count-data approaches. From an ecological perspective, the results suggest that thermal conditions and microtopography play important roles in shaping reproductive patterns. The strong negative effect of maximum temperature indicates that elevated thermal conditions may constrain reproductive investment or nesting success, while the positive association with elevation suggests that slightly higher sites provide more favorable microhabitat conditions. These findings provide a preliminary basis for the more specialized modeling approaches applied in subsequent analyses.

5.2.2. Poisson generalized linear model

Given that egg number represents a discrete count variable, a GLM with a Poisson distribution and logarithmic link function was adopted as the primary inferential framework. The model included the predictors retained during the exploratory phase: precipitation, cloud cover, maximum temperature, elevation, minimum distance to the high tide line, and minimum distance to vegetation. The base Poisson GLM showed an adequate fit and confirmed the patterns identified during the exploratory analysis. Maximum temperature exhibited a significant negative association with egg number ($\beta = -0.036 \pm 0.013$, $p = 0.005$), indicating that higher temperatures were associated with lower expected egg counts. Elevation showed a positive but non-significant effect under classical variance estimates ($\beta = 0.075 \pm 0.066$, $p = 0.250$). The remaining predictors did not show statistically detectable effects.

Model diagnostics indicated that the Poisson distribution adequately represented the data. Overdispersion was evaluated using both the residual deviance and Pearson chi-square ratios relative to their degrees of freedom. Both ratios were approximately 0.25, well below one, indicating no evidence of overdispersion and suggesting that the variance was not greater than expected under the Poisson process. Model fit was further assessed using the Cox and Snell pseudo-R^2, which was 0.136. Although lower than the coefficient of determination typically observed in linear regression models, pseudo-R^2 values of this magnitude are common in ecological count data, where variability is driven by multiple environmental and stochastic factors.

As a precautionary step, an additional specification was estimated using heteroskedasticity-consistent (HC3) robust standard errors to obtain more conservative inference. This approach accounts for potential unobserved heterogeneity associated with the ecological structure of the dataset, including multiple species

and uneven sampling across sites. Robust variance estimators adjust standard errors without altering coefficient estimates. This increases the reliability of statistical inference under mild model misspecification. Under the robust specification (Table 3), coefficient estimates remained unchanged, but standard errors were reduced. Maximum temperature remained strongly significant ($\beta = -0.036 \pm 0.006$, $p < 0.001$), reinforcing the negative thermal effect on egg abundance. Elevation became statistically significant ($\beta = 0.075 \pm 0.029$, $p = 0.008$), suggesting that nests at higher elevations tend to contain slightly larger clutches. Precipitation and distance to the high tide line showed marginal negative effects ($p \approx 0.07$-0.09), while cloud cover and distance to vegetation remained non-significant. Importantly, the use of robust standard errors did not alter the magnitude or direction of the estimated coefficients, only the associated uncertainty. This confirms that the main ecological signal, the negative effect of maximum temperature, is stable across variance specifications. Because the robust formulation provides more conservative inference while preserving model structure, it was retained as the preferred specification for interpretation.

Table 3. Parameter estimates (β), robust standard errors (HC3), and p-values for the robust Poisson GLM.

	β	std err	p
Constant	1.674	0.156	<0.001
Minimum distance to vegetation	0.001	0.001	0.527
Minimum distance to high tide	-0.001	0.001	0.094
Cloud cover	-0.001	0.002	0.290
Maximum temperature	-0.036	0.006	<0.001
Precipitation	-0.016	0.009	0.069
Elevation	0.075	0.029	0.008

To evaluate whether these relationships were influenced by interspecific or spatial variation, additional models were fitted including species and site as categorical predictors (separately and jointly), all estimated using robust standard errors. Across these specifications, model fit showed only modest variation, with pseudo-R^2 values ranging from approximately 0.137 to 0.176. In all cases, maximum temperature remained strongly negative and highly significant ($p < 0.001$), indicating a consistent thermal effect across species and sites. Elevation retained a positive effect and was generally significant or marginally significant ($p \approx 0.02$-0.05), suggesting that nests located at slightly higher elevations tend to contain more eggs. Although incorporating species slightly increased the explanatory power of the model and revealed some differences in clutch size among taxa, the inclusion of site explained little additional variation and none of the site coefficients were statistically significant. The combined model including both species and site produced only a minor improvement in fit while substantially increasing model complexity relative to sample size. Overall, these results indicate that the negative effect of maximum temperature and the positive association with elevation are robust across ecological contexts. Because categorical predictors did not substantially

improve model performance, the more parsimonious Poisson GLM including only continuous predictors was retained as the primary model for ecological interpretation.

5.2.3. Exploratory extensions: mixed-effects and non-linear models

Exploratory extensions of the Poisson GLM were conducted to evaluate two additional aspects of the data structure: potential intra-group dependence associated with hierarchical sampling and the possibility of non-linear responses along environmental gradients. First, GLMMs were explored by incorporating species and site as random effects to account for potential dependence among observations within groups. However, these models proved numerically unstable and failed to converge reliably, likely due to the limited number of levels in each grouping factor (four species and four sites). Diagnostic output indicated convergence warnings and unstable variance estimates for the random components. This suggests that the data structure did not support reliable estimation of random effects. The inclusion of random effects also did not substantially alter the direction or magnitude of the fixed coefficients observed in the Poisson GLM. For these reasons, GLMMs were considered exploratory and were not used for final inference.

Second, GAMs with a Poisson distribution were fitted to assess potential non-linear relationships between predictors and egg abundance. GAMs allow flexible estimation of predictor effects through smooth functions. They are commonly used to detect threshold responses or complex ecological gradients. Smooth terms were fitted for the two primary predictors identified in the GLM: maximum temperature and elevation. The results confirmed a statistically significant effect of maximum temperature, with the smooth function indicating a monotonic decline in expected egg number as temperature increased. In contrast, elevation showed no evidence of a non-linear effect, suggesting that its influence is adequately captured by a linear term. Allowing non-linear smooth functions did not reveal additional structure beyond that identified by the Poisson GLM.

Taken together, these results indicate that neither hierarchical random effects nor non-linear predictor responses substantially improved model performance. The relationships identified by the Poisson GLM, particularly the negative effect of maximum temperature and the positive association with elevation, remained consistent across alternative modeling frameworks. Consequently, the simpler Poisson GLM was retained as the final analytical model due to its stability, parsimony, and interpretability.

5.2.4. Non-parametric evaluation of predictor importance: Random Forest

To complement parametric analyses and evaluate predictor importance without assumptions about functional form or error distribution, a RF regression model was implemented as an exploratory machine learning approach (Figure 13). The RF analysis revealed a strong dominance of maximum temperature, which accounted for most of the model's predictive importance (≈ 0.81). All other predictors showed

substantially lower importance values, indicating secondary contributions to predictive performance. Among these, distance to vegetation (≈ 0.10) and distance to the high tide line (≈ 0.07) showed moderate importance. Cloud cover (≈ 0.05), elevation (≈ 0.04), and precipitation (≈ 0.02) contributed relatively little to overall predictive accuracy. The strong dominance of maximum temperature in the RF model corroborates the patterns identified in the Poisson GLM, which also highlighted temperature as the primary factor associated with variation in egg abundance. The consistency of this pattern across both parametric and non-parametric frameworks indicates that the influence of temperature is robust to modeling assumptions and represents the dominant driver within the dataset.

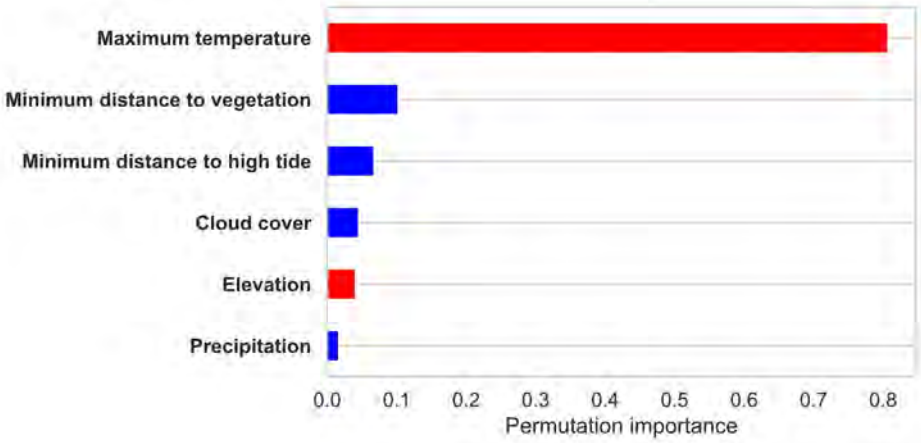

Figure 13. Permutation importance of main study predictors from the RF model. Variables highlighted in red indicate those identified as statistically significant in the Poisson GLM analyses.

Notably, elevation exhibited relatively low permutation importance in the RF analysis despite showing a statistically significant effect in the Poisson GLM. This difference reflects the complementary roles of the two approaches. While the GLM estimates marginal effects after controlling for other predictors, RF evaluates variables based on their contribution to predictive accuracy. In this context, the results suggest that elevation exerts a systematic but secondary influence on egg abundance, likely reflecting microtopographic variation in nesting habitat rather than a dominant driver. In sum, the RF results reinforce that maximum temperature is the principal factor associated with egg abundance, whereas other predictors play secondary roles. The convergence of results across parametric regression models, mixed and additive exploratory models, and a non-parametric machine learning framework provides strong support for the robustness of the temperature-egg abundance relationship identified in this study.

5.2.5. Ecological interpretation of model results

Statistical analyses consistently identified maximum temperature and elevation as the variables most strongly associated with variation in egg abundance across the Rockaway Peninsula. The Poisson regression model with robust standard errors revealed a clear negative relationship between maximum temperature and

egg abundance, while elevation showed a positive association. These patterns remained stable across alternative specifications and exploratory approaches, including models incorporating species and site effects, generalized additive models, and a Random Forest framework, although elevation showed relatively low predictive importance in the RF model despite its consistent statistical significance in regression-based approaches. The consistency of these results indicates that the temperature-reproduction relationship identified in this study is robust and not dependent on a specific modeling strategy.

The final Poisson model describes egg abundance as a function of maximum temperature and elevation and can be expressed as:

$$\text{Number of Eggs}_i = \exp\left(1.674 - 0.036 \cdot \text{Maximum Temperature}_i + 0.075 \cdot \text{Elevation}_i\right)$$

For small coefficients, β can be approximately interpreted as a percentage change, since $\exp(\beta) \approx 1 + \beta$. Under this formulation, each 1°C increase in maximum temperature is associated with an approximate 3.6% decrease in expected egg counts, whereas each unit increase in elevation corresponds to an increase of about 7-8%. These estimates summarize the combined effects of the two significant predictors. The model indicates that higher temperatures are associated with reduced reproductive output, while higher elevations are associated with modest increases in clutch size. Model performance is illustrated by the relationship between observed and predicted egg counts (Figure 14), where predicted values follow the central tendency of the data.

The predicted-observed relationship shows that the model captures the dominant clutch size range of the system, particularly between two and three eggs, which represent the most frequent clutch sizes across species. Although some dispersion around the 1:1 reference line is present, this is expected in ecological datasets where reproductive output varies among species, individuals, and environmental conditions. The model therefore reproduces the overall structure of the data while maintaining a parsimonious set of predictors.

From an ecological perspective, the negative effect of maximum temperature indicates that thermal conditions act as a key constraint for beach-nesting shorebirds. Eggs develop in exposed substrates where ambient temperature and solar radiation strongly influence incubation conditions. As temperatures increase, adults must invest more energy in thermoregulatory behaviors such as shading eggs or adjusting incubation posture, which can reduce incubation efficiency and potentially limit reproductive investment. This interpretation is supported by observed phenological patterns, where reproductive activity peaked at intermediate temperatures and declined during warmer periods.

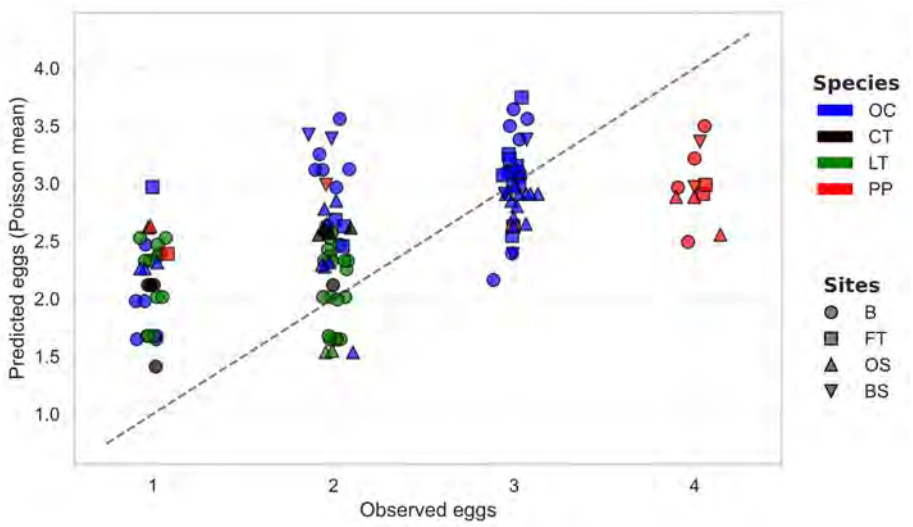

Figure 14. Predicted vs. observed egg counts.

Elevation, although less dominant than temperature, emerged as a consistent spatial factor shaping nesting conditions. Higher positions along the beach profile reduce the risk of tidal flooding and storm overwash, which are major causes of nest failure in coastal systems. Descriptive analyses showed that most nests occurred at intermediate elevations, suggesting active selection of microtopographic conditions that balance flooding risk and habitat availability. Even small differences in elevation can substantially influence nest survival in barrier beach environments.

The combined influence of temperature and elevation highlights the interaction between climatic stress and coastal geomorphology in shaping reproductive outcomes. Temperature operates as a regional constraint affecting incubation conditions, whereas elevation acts at a finer spatial scale by defining the microhabitat experienced by nests. Together, these factors determine the thermal and hydrological environment in which eggs develop.

Broader descriptive analyses provide additional context for these relationships. Nest distribution patterns reflected contrasting reproductive strategies among species, with colonial breeders (e.g., terns) forming dense clusters and territorial species (e.g., PP) maintaining greater spacing. Nest placement relative to the high tide line, vegetation, and human infrastructure further indicates that birds balance multiple environmental pressures when selecting nesting sites. These processes likely interact with temperature and elevation to shape overall habitat suitability across the peninsula.

Overall, shorebird reproductive patterns on the Rockaway Peninsula are structured by the combined effects of thermal conditions and coastal microtopography within a heterogeneous and human-influenced landscape. As coastal systems experience rising temperatures, sea-level rise, and increasing storm intensity,

these drivers are likely to play an increasingly important role in determining reproductive success and spatial distribution of beach-nesting bird communities.

6. Conclusion

This study evaluated the environmental, atmospheric, and spatial drivers of egg abundance and nesting patterns of beach-nesting shorebirds across four geomorphologically distinct sites of the Rockaway Peninsula, a heterogeneous urban coastal system characterized by variation in habitat structure, human disturbance, and microclimate. By combining descriptive ecological analyses with statistical modeling, this study provides an integrated perspective on how environmental conditions and habitat configuration influence reproductive patterns within this barrier beach system.

Descriptive analyses revealed clear spatial organization of nesting communities. Colonial species such as Common Tern and Least Tern formed dense clusters, whereas territorial species such as Piping Plover and American Oystercatcher maintained greater spacing between nests. Nest placement relative to coastal features indicates that birds balance multiple environmental pressures when selecting nesting sites, including flooding risk, predator detection, and proximity to human infrastructure. Differences in distances to the high tide line, vegetation, roads, and buildings highlight the combined influence of geomorphology and urbanization on nest distribution.

The Poisson GLM with robust standard errors identified maximum temperature as the dominant factor associated with variation in egg abundance. The negative relationship between maximum temperature and egg count indicates that thermal conditions constrain reproductive investment, likely reflecting increased thermal stress on eggs and higher energetic demands on incubating adults. This pattern remained consistent across alternative modeling approaches, including models incorporating species and site effects, generalized additive models, and Random Forest analyses.

Elevation showed a statistically significant but more moderate effect and lower predictive importance in the RF model. This pattern suggests that elevation contributes to nesting habitat suitability by reducing flooding risk and improving substrate stability, although it does not dominate variation in egg abundance at the scale of the study. Descriptive analyses support this interpretation, showing that nests were generally located at intermediate elevations where flooding risk is reduced while suitable substrate remains available.

Other variables, including precipitation, cloud cover, and distances to natural features, played secondary roles in the statistical models, suggesting that their effects may operate at finer spatial scales or influence other components of reproductive success not captured directly by egg abundance. Descriptive patterns

nonetheless indicate that habitat structure and anthropogenic features shape the broader spatial configuration of nesting habitats.

Several limitations should be acknowledged. First, the analysis was conducted within a single urban coastal system and based on a single breeding season, which may limit generalizability across regions or years. Second, the response variable focused on egg abundance and did not include later stages of reproduction such as hatching success or chick survival, which may respond differently to environmental drivers. Despite these limitations, the results provide clear evidence that thermal conditions and coastal microtopography are key factors shaping reproductive patterns of beach-nesting shorebirds in the Rockaway Peninsula. Identifying temperature as a dominant driver has important implications for conservation and management, particularly under scenarios of climate warming and increasing thermal stress in exposed coastal habitats. Overall, this study highlights the value of integrating ecological observations with complementary statistical and machine-learning approaches to better understand the drivers of reproduction in dynamic coastal ecosystems.

7. Management and conservation implications

The results of this study have important implications for the management and conservation of beach-nesting shorebirds in dynamic barrier island environments such as the Rockaway Peninsula. These coastal systems are shaped by interactions among geomorphological processes, climatic conditions, and human activities, all of which influence the availability and quality of nesting habitat. Effective conservation therefore requires an integrated understanding of both ecological drivers and anthropogenic pressures.

Statistical analyses indicate that thermal conditions, particularly maximum temperature, represent a dominant factor associated with variation in egg abundance. As global temperatures rise, climate change is expected to increasingly influence the reproductive ecology of migratory birds by altering breeding phenology, physiological stress, and resource availability (Kumar et al., 2024). In exposed coastal environments, elevated temperatures may intensify thermal stress on incubating adults and developing embryos, potentially reducing reproductive investment and breeding success. Management approaches should therefore consider the effects of increasing thermal extremes, including maintaining habitat heterogeneity that allows birds to select microhabitats with more favorable thermal conditions.

Habitat structure and geomorphological processes also play a critical role in determining the availability of suitable nesting environments. Barrier island landscapes are shaped by storms, overwash, and sediment dynamics, which periodically create sparsely vegetated habitats preferred by many beach-nesting species (Zeigler et al., 2019). Natural disturbances can thus generate early-successional habitats that support reproduction. However, coastal stabilization, dune construction, and vegetation management aimed at

protecting infrastructure may reduce the availability of these habitats by limiting overwash processes and accelerating vegetation succession (Cohen, 2005; Schupp et al., 2013). Conservation strategies that maintain some degree of natural geomorphological dynamics, such as allowing overwash in selected areas or managing vegetation to preserve open sandy habitats, may enhance nesting habitat availability.

Human disturbance represents another major concern in recreational coastal landscapes. Pedestrian activity and off-road vehicles can alter shorebird behavior, reduce nest attendance, and increase energetic costs for incubating adults (Felton et al., 2018). Long-term monitoring has also shown strong relationships between human activity and population trends in species such as the Piping Plover (Kwon et al., 2021). Seasonal access restrictions, protective buffers around nesting areas, and public awareness programs are therefore key measures for reducing disturbance during the breeding season and improving reproductive outcomes. In addition to disturbance management, predator control and habitat quality management are often necessary to maintain reproductive success. Predation and flooding are key drivers of nest and chick survival in several shorebird species, including the American Oystercatcher (Call et al., 2026). Actions such as predator monitoring, targeted control, and habitat modifications that reduce predator access can contribute to improving productivity in nesting populations.

Long-term ecological monitoring is essential for evaluating conservation effectiveness and understanding population responses to environmental change. Monitoring programs that track population size, reproductive success, habitat conditions, and disturbance provide critical information for adaptive management (Brush et al., 2019). Standardized monitoring across breeding, migration, and wintering stages is particularly important for migratory species influenced by conditions throughout their annual cycle.

The dynamic nature of barrier island ecosystems highlights the importance of ecosystem-based management approaches that balance coastal protection, habitat conservation, and human use. Actions aimed solely at stabilizing coastlines may conflict with ecological processes that generate suitable habitat, leading to trade-offs between infrastructure protection and biodiversity conservation (Biel et al., 2017). Integrating ecological considerations into coastal planning, such as incorporating habitat restoration into beach nourishment projects or maintaining open sandy areas within developed coastlines, can help reduce these trade-offs.

In summary, the findings highlight the importance of considering climatic conditions, coastal geomorphology, and human disturbance when designing conservation strategies for beach-nesting shorebirds. As climate change and coastal development continue to reshape barrier island environments, adaptive management approaches that integrate ecological monitoring, habitat restoration, and disturbance mitigation will be critical for sustaining shorebird populations in urbanized coastal systems.

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References

Abernathy, V. E., Good, A., Blanchard, A., Bongiovanni, M., Bonds, E., Warner, H., Chaknis, E., Pulsifer, G., & Huntley, F. (2023). The Effects of Climate Change on the Nesting Phenology of Three Shorebird Species in the United States. *Animals*, *13*(15), 2459. https://doi.org/10.3390/ani13152459

Althouse, M. A., Cohen, J. B., Karpanty, S. M., Spendelow, J. A., Davis, K. L., Parsons, K. C., & Luttazi, C. F. (2019). Evaluating response distances to develop buffer zones for staging terns. *The Journal of Wildlife Management*, *83*(2), 260–271. https://doi.org/10.1002/jwmg.21594

Andes, A. K., Sherfy, M. H., Shaffer, T. L., & Ellis-Felege, S. N. (2020). Plasticity of Least Tern and Piping Plover nesting behaviors in response to sand temperature. *Journal of Thermal Biology*, *91*, 102579. https://doi.org/10.1016/j.jtherbio.2020.102579

Anteau, M. J., Wiltermuth, M. T., Sherfy, M. H., & Shaffer, T. L. (2014). Measuring and predicting abundance and dynamics of habitat for piping plovers on a large reservoir. *Ecological Modelling*, *272*, 16–27. https://doi.org/10.1016/j.ecolmodel.2013.08.020

Arndtsen, C. (2022). *The Role of Nest Location on the Reproductive Success of Piping Plovers Breeding at Rockaway Beach, New York* [Master's Thesis, Hunter College, City University of New York]. https://academicworks.cuny.edu/hc_sas_etds/927

Arnold, J. M., Oswald, S. A., Nisbet, I. C. T., Pyle, P., & Patten, M. A. (2020). Common Tern (Sterna hirundo), version 1.0. *Birds of the World*. https://doi.org/10.2173/bow.comter.01

Atwood, J. L., & Massey, B. W. (1988). Site Fidelity of Least Terns in California. *The Condor: Ornithological Applications*, *90*(2), 389–394. https://doi.org/10.2307/1368567

Baasch, D. M., Farrell, P. D., Farnsworth, J. M., & Smith, C. B. (2017). Nest-site selection by Interior Least Terns and Piping Plovers at managed, off-channel sites along the Central Platte River in Nebraska, USA. *Journal of Field Ornithology*, *88*(3), 236–249. https://doi.org/10.1111/jofo.12206

Baker, A., & Michael, C. (1980). Breeding Schedule, Clutch Size and Egg Size of American Oystercatchers Haematopus Palliatus in Virginia. *Wader Study Group Bulletin*, *30*(1), 32–33. https://digitalcommons.usf.edu/wsg_bulletin/vol30/iss1/30

Bearmore, B., Ozolin, B., & Sacks, P. (2016). Fort Tilden Historical Bulkhead Assessment. *American Society of Civil Engineers*, 744–751. https://doi.org/10.1061/9780784479919.077

Bergstrom, P., & Terwilliger, K. (1987). Nest Sites and Aggressive Behaviour of Piping and Wilsons Plovers in Virginia: Some Preliminary Results. *Wader Study Group Bulletin*, *50*(1), 35–39. https://digitalcommons.usf.edu/wsg_bulletin/vol50/iss1/18

Biel, R. G., Hacker, S. D., Ruggiero, P., Cohn, N., & Seabloom, E. W. (2017). Coastal protection and conservation on sandy beaches and dunes: Context-dependent tradeoffs in ecosystem service supply. *Ecosphere*, *8*(4), e01791. https://doi.org/10.1002/ecs2.1791

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J.-S. S. (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology & Evolution*, *24*(3), 127–135. https://doi.org/10.1016/j.tree.2008.10.008

Borneman, T. E., Rose, E. T., & Simons, T. R. (2016). Off-road vehicles affect nesting behaviour and reproductive success of American Oystercatchers Haematopus palliatus. *Ibis*, *158*(2), 261–278. https://doi.org/10.1111/ibi.12358

Brush, J. M., Pruner, R. A., & Driscoll, M. J. L. (2019). GoMAMM Strategic Bird Monitoring Guidelines: Shorebirds. In R. R. Wilson, A. M. V. Fournier, J. S. Gleason, J. E. Lyons, & M. S. Woodrey (Eds.), *Strategic Bird Monitoring Guidelines for the Northern Gulf of Mexico* (1st ed., pp. 171–202). Mississippi Agricultural and Forestry Experiment Station Research Bulletin 1228.

Burger, J. (1987). Physical and Social Determinants of Nest-Site Selection in Piping Plover in New Jersey. *The Condor: Ornithological Applications*, *89*(4), 811–818. https://doi.org/10.2307/1368529

Burger, J., & Gochfeld, M. (1988). Nest-Site Selection and Temporal Patterns in Habitat Use of Roseate and Common Terns. *The Auk*, *105*(3), 433–438. https://doi.org/10.1093/auk/105.3.433

Burger, J., & Lesser, F. (1978). Selection of Colony Sites and Nest Sites by Common Terns Sterna Hirundo in Ocean County, New Jersey. *Ibis*, *120*(4), 433–449. https://doi.org/10.1111/j.1474-919X.1978.tb06810.x

Cairns, W. E. (1982). Biology and Behavior of Breeding Piping Plovers. *The Wilson Bulletin*, *94*(4), 531–545. https://www.biodiversitylibrary.org/part/209562

Caliendo, V., Kleyheeg, E., Beerens, N., Camphuysen, K. C. J., Cazemier, R., Elbers, A. R. W., Fouchier, R. A. M., Kelder, L., Kuiken, T., Leopold, M., Slaterus, R., Spierenburg, M. A. H., van der Jeugd, H., Verdaat, H., & Rijks, J. M. (2024). Effect of 2020–21 and 2021–22 Highly Pathogenic Avian Influenza H5 Epidemics on Wild Birds, the Netherlands. *Emerging Infectious Diseases*, *30*(1), 50–57. https://doi.org/10.3201/eid3001.230970

Call, M. N. (2025). *Shorebirds in a changing landscape: Assessing the top-down and bottom-up drivers of American oystercatcher (Haematopus palliatus) reproductive success in the Virginia barrier islands* [PhD Thesis, Virginia Tech]. https://hdl.handle.net/10919/141160

Call, M. N., Wilke, A. L., Wails, C. N., Lapenta, K. C., Karpanty, S. M., Fraser, J. D., & Denmon, P. (2026). Flooding and a complex predator community drive American oystercatcher nest and chick survival in Virginia. *The Journal of Wildlife Management*, *90*(2), e70145. https://doi.org/10.1002/jwmg.70145

Cameron, A. C., & Trivedi, P. K. (2013). *Regression Analysis of Count Data* (2nd ed.). Cambridge University Press. https://doi.org/10.1017/CBO9781139013567

Claassen, A. H., Arnold, T. W., Roche, E. A., Saunders, S. P., & Cuthbert, F. J. (2014). Factors influencing nest survival and renesting by Piping Plovers in the Great Lakes region. *The Condor: Ornithological Applications*, *116*(3), 394–407. https://doi.org/10.1650/CONDOR-13-146.1

Clements, S. J., Loghry, J. P., Ballard, B. M., & Weegman, M. D. (2022). Carry-over effects of weather and decision-making on nest success of a migratory shorebird. *Ecology and Evolution*, *12*(12), e9581. https://doi.org/10.1002/ece3.9581

Coch, N. K. (2015). Unique Vulnerability of the New York–New Jersey Metropolitan Area to Hurricane Destruction. *Journal of Coastal Research*, *31*(1), 196–212. https://doi.org/10.2112/JCOASTRES-D-13-00183.1

Cohen, J. B. (2005). *Factors Limiting Piping Plover Nesting Pair Density and Reproductive Output on Long Island, New York* [PhD Thesis, Virginia Tech]. http://hdl.handle.net/10919/27414

Cohen, J. B., Houghton, L. M., & Fraser, J. D. (2009). Nesting Density and Reproductive Success of Piping Plovers in Response to Storm- and Human-Created Habitat Changes. *Wildlife Monographs*, *173*(1), 1–24. https://doi.org/10.2193/2007-553

Dinsmore, S. J. (2019). Population Biology. In M. A. Cowell & S. M. Haig (Eds.), *The Population Ecology and Conservation of Charadrius Plovers* (1st ed., pp. 245–274). CRC Press.

Durbin, J., & Watson, G. S. (1950). Testing for serial correlation in least squares regression I. *Biometrika*, *37*(3–4), 409–428. https://doi.org/10.1093/biomet/37.3-4.409

Elliott-Smith, E., & Haig, S. M. (2020). Piping Plover (Charadrius melodus), version 1.0. *Birds of the World*. https://doi.org/10.2173/bow.pipplo.01

Erwin, R. M., Sanders, G. M., Prosser, D. J., & Cahoon, D. R. (2006). High tides and rising seas: Potential effects on estuarine waterbirds. In R. Greenberg, J. Maldonado, S. Droege, & M. V. McDonald (Eds.), *Terrestrial vertebrates of tidal marshes: Evolution, ecology, and conservation. Studies in Avian Biology No. 32* (1st ed., pp. 214–228). Cooper Ornithological Society.

Farnsworth, J. M., Baasch, D. M., & Farrell, P. D. (2018). Integrating species-centric and geomorphic-centric views of interior least tern and piping plover habitat selection. *Heliyon*, *4*(6), e00648. https://doi.org/10.1016/j.heliyon.2018.e00648

Farrell, P., Baasch, D., Farnsworth, J., & Smith, C. (2018). Avian Conservation and Ecology: Interior Least Tern and Piping Plover nest and brood survival at managed, off-channel sites along the central Platte

River, Nebraska, USA 2001-2015. *Avian Conservation and Ecology*, *13*(1). https://doi.org/10.5751/ACE-01133-130101

Felton, S. K., Pollock, K. H., & Simons, T. R. (2018). Response of beach-nesting American Oystercatchers to off-road vehicles: An experimental approach reveals physiological nuances and decreased nest attendance. *The Condor: Ornithological Applications*, *120*(1), 47–62. https://doi.org/10.1650/CONDOR-17-84.1

Fisher, A., Rudin, C., & Dominici, F. (2019). All Models are Wrong, but Many are Useful: Learning a Variable's Importance by Studying an Entire Class of Prediction Models Simultaneously. *Journal of Machine Learning Research*, *20*, 1–81. https://jmlr.csail.mit.edu/papers/volume20/18-760/18-760.pdf

Forman, R. T. T., Reineking, B., & Hersperger, A. M. (2002). Road Traffic and Nearby Grassland Bird Patterns in a Suburbanizing Landscape. *Environmental Management*, *29*(6), 782–800. https://doi.org/10.1007/s00267-001-0065-4

Forsberg, E. M. (2024). *Demographic Consequences of Off-river Nesting for Piping Plover (Charadrius melodus) and Interior Least Tern (Sternula antillarum athalassos) in the Lower Platte River System, Nebraska* [Master's Thesis, University of Nebraska]. https://digitalcommons.unl.edu/natresdiss/377/

Forys, E. A., & Borboen-Abrams, M. (2006). Roof-top Selection by Least Terns in Pinellas County, Florida. *Waterbirds*, *29*(4), 501–506. https://doi.org/10.1675/1524-4695(2006)29%5B501:RSBLTI%5D2.0.CO;2

Galbraith, H., DesRochers, D. W., Brown, S., & Reed, J. M. (2014). Predicting Vulnerabilities of North American Shorebirds to Climate Change. *PLOS ONE*, *9*(9), e108899. https://doi.org/10.1371/journal.pone.0108899

Garvey, M. E., Nol, E., Howerter, D. W., & Armstrong, L. M. (2013). A Spatial Analysis of Factors Affecting Nesting Success of Shorebirds in the Canadian Prairies. *The Condor: Ornithological Applications*, *115*(1), 58–66. https://doi.org/10.1525/cond.2012.110146

Ghasemi, A., & Zahediasl, S. (2012). Normality Tests for Statistical Analysis: A Guide for Non-Statisticians. *International Journal of Endocrinology and Metabolism*, *10*(2), 486–489. https://doi.org/10.5812/ijem.3505

Gochfeld, M. (1977). Intraclutch Egg Variation: The Uniqueness of the Common Tern's Third Egg. *Bird Banding*, *48*(4), 325–332. https://digitalcommons.usf.edu/bird_banding/vol48/iss4/4

Gomes, D. G. E. (2022). Should I use fixed effects or random effects when I have fewer than five levels of a grouping factor in a mixed-effects model? *PeerJ*, *10*, e12794. https://doi.org/10.7717/peerj.12794

Graells, G., Celis-Diez, J. L., Corcoran, D., & Gelcich, S. (2022). Bird Communities in Coastal Areas. Effects of Anthropogenic Influences and Distance From the Coast. *Frontiers in Ecology and Evolution*, *10*, 1–10. https://doi.org/10.3389/fevo.2022.807280

Greenlees, K. (2020). *Panarchy on the Peninsula: Rockaways' Risk, Response and Resilience Following Superstorm Sandy* [Bachelor's Thesis, Vassar College]. https://doi.org/10.13140/RG.2.2.28956.92807

Guild, R., Wang, X., Hirtle, S., & Mader, S. (2024). Spatiotemporal and weather effects on the reproductive success of piping plovers on Prince Edward Island, Canada. *Ecology and Evolution*, *14*(8), e11581. https://doi.org/10.1002/ece3.11581

Gujarati, D. N., & Porter, D. C. (2009). *Basic Econometrics* (5th ed.). McGraw-Hill Education.

Harrison, X. A., Donaldson, L., Correa-Cano, M. E., Evans, J., Fisher, D. N., Goodwin, C. E. D., Robinson, B. S., Hodgson, D. J., & Inger, R. (2018). A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ*, *6*, e4794. https://doi.org/10.7717/peerj.4794

Hastie, T., Tibshirani, R., & Friedman, J. (2009). *The Elements of Statistical Learning* (2nd ed.). Springer. https://doi.org/10.1007/978-0-387-84858-7

Hilbe, J. M. (2011). *Negative Binomial Regression* (2nd ed.). Cambridge University Press. https://doi.org/10.1017/CBO9780511973420

Janda, C. N., Warrick, J. A., Buscombe, D., & Batiste, S. (2025). Shoreline Change of Western Long Island, New York, from Satellite-Derived Shorelines. *Coasts*, *5*(2), 1–29. https://doi.org/10.3390/coasts5010002

Klaassen, M., & Wille, M. (2023). The plight and role of wild birds in the current bird flu panzootic. *Nature Ecology & Evolution*, *7*(10), 1541–1542. https://doi.org/10.1038/s41559-023-02182-x

Koleček, J., Reif, J., Šálek, M., Hanzelka, J., Sottas, C., & Kubelka, V. (2021). Global population trends in shorebirds: Migratory behaviour makes species at risk. *Die Naturwissenschaften*, *108*(9), 1–8. https://doi.org/10.1007/s00114-021-01717-1

Korne, N., Flemming, S. A., Smith, P. A., & Nol, E. (2020). Applying structure-from-motion habitat reconstruction and GIS terrain analysis to test hypotheses about nest-site selection by shorebirds. *Journal of Field Ornithology*, *91*(4), 421–432. https://doi.org/10.1111/jofo.12351

Krogh, M. G., & Schweitzer, S. H. (1999). Least Terns Nesting on Natural and Artificial Habitats in Georgia, USA. *Waterbirds: The International Journal of Waterbird Biology*, *22*(2), 290–296. https://doi.org/10.2307/1522218

Kumar, S., Kler, T. K., Sekhon, G. S., & Sahni, T. (2024). Impacts on avian migratory patterns due to climate change and hormonal disruption: A review. *Mitigation and Adaptation Strategies for Global Change*, *29*(7), 69. https://doi.org/10.1007/s11027-024-10163-z

Kwon, E., English, W. B., Weiser, E. L., Franks, S. E., Hodkinson, D. J., Lank, D. B., & Sandercock, B. K. (2018). Delayed egg-laying and shortened incubation duration of Arctic-breeding shorebirds coincide with climate cooling. *Ecology and Evolution*, *8*(2), 1339–1351. https://doi.org/10.1002/ece3.3733

Kwon, E., Robinson, S., Weithman, C. E., Catlin, D. H., Karpanty, S. M., Altman, J., Simons, T. R., & Fraser, J. D. (2021). Contrasting long-term population trends of beach-nesting shorebirds under shared environmental pressures. *Biological Conservation*, *260*, 109178. https://doi.org/10.1016/j.biocon.2021.109178

Lauro, B., & Burger, J. (1989). Nest-Site Selection of American Oystercatchers (Haematopus palliatus) in Salt Marshes. *The Auk*, *106*(2), 185–192. https://www.jstor.org/stable/4087710

Leroy, F., Jarzyna, M. A., & Keil, P. (2026). Acceleration hotspots of North American birds' decline are associated with agriculture. *Science*, *391*(6788), 917–921. https://doi.org/10.1126/science.ads0871

Lostritto, P., & Taylor, G. (2015). Effects of Sea Level Rise on Foraging Habitat of the Piping Plover (charadrius Melodus): A Geographic Information Systems Approach. *Maryland Birdlife*, *64*(1), 23–41. https://digitalcommons.usf.edu/maryland_birdlife/vol64/iss1/2

Maslo, B., Leu, K., Faillace, C., Weston, M. A., Pover, T., & Schlacher, T. A. (2016). Selecting umbrella species for conservation: A test of habitat models and niche overlap for beach-nesting birds. *Biological Conservation*, *203*, 233–242. https://doi.org/10.1016/j.biocon.2016.09.012

Maslo, B., Leu, K., Pover, T., Weston, M. A., & Schlacher, T. A. (2018). Managing birds of conservation concern on sandy shores: How much room for future conservation actions is there? *Ecology and Evolution*, *8*(22), 10976–10988. https://doi.org/10.1002/ece3.4564

Mazzocchi, A., & Forys, E. (2005). Nesting Habitat Selection of the Least Tern on the Gulf Coast of Florida. *Florida Field Naturalist*, *33*(3), 71–80. https://digitalcommons.usf.edu/ffn/vol33/iss3/1

McCullagh, P., & Nelder, J. A. (1989). *Generalized Linear Models* (2nd ed.). Chapman and Hall. https://doi.org/10.1201/9780203753736

McGuire, R. L., Lanctot, R. B., Saalfeld, S. T., Ruthrauff, D. R., & Liebezeit, J. R. (2020). Shorebird Reproductive Response to Exceptionally Early and Late Springs Varies Across Sites in Arctic Alaska. *Frontiers in Ecology and Evolution*, *8*, 1–19. https://doi.org/10.3389/fevo.2020.577652

Montgomery, D. C., Peck, E. A., & Vining, G. G. (2012). *Introduction to Linear Regression Analysis* (5th ed.). John Wiley & Sons.

Neate-Clegg, M. H. C., Tonelli, B. A., & Tingley, M. W. (2024). Advances in breeding phenology outpace latitudinal and elevational shifts for North American birds tracking temperature. *Nature Ecology & Evolution*, *8*(11), 2027–2036. https://doi.org/10.1038/s41559-024-02536-z

New York State Department of Environmental Conservation. (2026). *Animals, Fish, & Plants—NYSDEC*. https://dec.ny.gov/nature/animals-fish-plants

New York State GIS Clearinghouse. (2024). *New York City Orthoimagery Downloads*. https://gis.ny.gov/new-york-city-orthoimagery-downloads

NOAA. (2026). *Data Search | National Centers for Environmental Information (NCEI)*. https://www.ncei.noaa.gov/access/search/data-search/local-climatological-data?pageNum=1&startDate=2025-04-01T00:00:00&endDate=2025-08-31T23:59:59&stations=74486094789

Nol, E., Baker, A. J., & Cadman, M. D. (1984). Clutch Initiation Dates, Clutch Size, and Egg Size of the American Oystercatcher in Virginia. *The Auk*, *101*(4), 855–867. https://doi.org/10.2307/4086913

Orton, P. M., Sanderson, E. W., Talke, S. A., Giampieri, M., & MacManus, K. (2020). Storm tide amplification and habitat changes due to urbanization of a lagoonal estuary. *Natural Hazards and Earth System Sciences*, *20*(9), 2415–2432. https://doi.org/10.5194/nhess-20-2415-2020

Palomino, D., & Carrascal, L. M. (2007). Threshold distances to nearby cities and roads influence the bird community of a mosaic landscape. *Biological Conservation*, *140*(1), 100–109. https://doi.org/10.1016/j.biocon.2007.07.029

Panigrahi, N. (2014). *Computing in Geographic Information Systems* (1st ed.). CRC Press.

Pearce-Higgins, J. W., Brown, D. J., Douglas, D. J. T., Alves, J. A., Bellio, M., Bocher, P., Buchanan, G. M., Clay, R. P., Conklin, J., Crockford, N., Dann, P., Elts, J., Friis, C., Fuller, R. A., Gill, J. A., Gosbell, K., Johnson, J. A., Marquez-Ferrando, R., Masero, J. A., … Verkuil, Y. I. (2017). A global threats overview for Numeniini populations: Synthesising expert knowledge for a group of declining migratory birds. *Bird Conservation International*, *27*(1), 6–34. https://doi.org/10.1017/S0959270916000678

Pendleton, E. A., Thieler, E. R., & Williams, S. J. (2005). Coastal vulnerability assessment of Gateway National Recreation Area (GATE) to sea-level rise. In *Open-File Report* (Nos. 2004–1257). U.S. Geological Survey. https://doi.org/10.3133/ofr20041257

Powell, A. N. (2001). Habitat Characteristics and Nest Success of Snowy Plovers Associated with California Least Tern Colonies. *The Condor: Ornithological Applications*, *103*(4), 785–792. https://doi.org/10.1093/condor/103.4.785

Ramey, A. M., Hill, N. J., DeLiberto, T. J., Gibbs, S. E. J., Camille Hopkins, M., Lang, A. S., Poulson, R. L., Prosser, D. J., Sleeman, J. M., Stallknecht, D. E., & Wan, X.-F. (2022). Highly pathogenic avian influenza is an emerging disease threat to wild birds in North America. *The Journal of Wildlife Management*, *86*(2), e22171. https://doi.org/10.1002/jwmg.22171

Razali, N. M., & Wah, Y. B. (2011). Power comparisons of Shapiro-Wilk, Kolmogorov-Smirnov, Lilliefors and Anderson-Darling tests. *Journal of Statistical Modeling and Analytics*, *2*(1), 21–33. https://www.nrc.gov/docs/ml1714/ml17143a100.pdf

Rodgers Jr., J. A., & Smith, H. T. (1995). Set-Back Distances to Protect Nesting Bird Colonies from Human Disturbance in Florida. *Conservation Biology*, *9*(1), 89–99. https://doi.org/10.1046/j.1523-1739.1995.09010089.x

Rosenberg, K. V., Dokter, A. M., Blancher, P. J., Sauer, J. R., Smith, A. C., Smith, P. A., Stanton, J. C., Panjabi, A., Helft, L., Parr, M., & Marra, P. P. (2019). Decline of the North American avifauna. *Science*, *366*(6461), 120–124. https://doi.org/10.1126/science.aaw1313

Ruiz de Alegría-Arzaburu, A., Garcia-Walther, J., Serratos, L. O., Vega, J. V., & Senner, N. R. (2025). The Impact of Beachface Morphology on Habitat Suitability and Breeding Success of Least Terns and Snowy Plovers. *Estuaries and Coasts*, *48*(5), 134. https://doi.org/10.1007/s12237-025-01574-5

Sæther, B.-E., & Engen, S. (2015). The concept of fitness in fluctuating environments. *Trends in Ecology & Evolution*, *30*(5), 273–281. https://doi.org/10.1016/j.tree.2015.03.007

Sanderson, E. W. (2016). Cartographic Evidence for Historical Geomorphological Change and Wetland Formation in Jamaica Bay, New York. *Northeastern Naturalist*, *23*(2), 277–304. https://doi.org/10.1656/045.023.0208

Schreiber, E. A., & Burger, J. (Eds.). (2001). *Biology of Marine Birds* (1st ed.). CRC Press. https://doi.org/10.1201/9781420036305

Schulte, S. A. (2012). *Ecology and Population Dynamics of American Oystercatchers (Haematopus palliatus)* [PhD Thesis, NC State University]. http://www.lib.ncsu.edu/resolver/1840.16/7678

Schulte, S. A., & Simons, T. R. (2015). Factors affecting the reproductive success of American Oystercatchers Haematopus palliatus on the Outer Banks of North Carolina. *Marine Ornithology*, *43*(1), 37–47. https://doi.org/10.5038/2074-1235.43.1.1099

Schupp, C. A., Winn, N. T., Pearl, T. L., Kumer, J. P., Carruthers, T. J. B., & Zimmerman, C. S. (2013). Restoration of overwash processes creates piping plover (*Charadrius melodus*) habitat on a barrier island (Assateague Island, Maryland). *Estuarine, Coastal and Shelf Science, EMECS9 Special Issue: Science-Based for Managing for Results*, *116*, 11–20. https://doi.org/10.1016/j.ecss.2012.07.003

Shapiro, S. S., & Wilk, M. B. (1965). An analysis of variance test for normality (complete samples). *Biometrika*, *52*(3–4), 591–611. https://doi.org/10.1093/biomet/52.3-4.591

Smith, A. C., & Edwards, B. P. M. (2021). North American Breeding Bird Survey status and trend estimates to inform a wide range of conservation needs, using a flexible Bayesian hierarchical generalized additive model. *Ornithological Applications*, *123*(1), duaa065. https://doi.org/10.1093/ornithapp/duaa065

Smith, P. A., Smith, A. C., Andres, B., Francis, C. M., Harrington, B., Friis, C., Morrison, R. I. G., Paquet, J., Winn, B., & Brown, S. (2023). Accelerating declines of North America's shorebirds signal the need for urgent conservation action. *Ornithological Applications*, *125*(2), duad003. https://doi.org/10.1093/ornithapp/duad003

Sterling, A. V. (2017). *Modeling productivity for American oystercatchers (haematopus palliatus) and Wilson's plovers (charadrius wilsonia) in a highly dynamic environment* [PhD Thesis, University of Georgia]. https://openscholar.uga.edu/record/15211

Stutzman, R. J., & Fontaine, J. J. (2015). Shorebird migration in the face of climate change: Potential shifts in migration phenology and resource availability. In E. M. Wood & J. L. Kellermann (Eds.),

Phenological synchrony and bird migration: Changing climate and seasonal resources in North America. (1st ed., pp. 145–159). CRC Press.

Suthar, A. R., Biggs, A. R., & Anderson, J. T. (2025). A Decadal Change in Shorebird Populations in Response to Temperature, Wind, and Precipitation at Hilton Head Island, South Carolina, USA. *Birds*, *6*(14), 1–20. https://doi.org/10.3390/birds6010014

Swayne, D. E., Sims, L. D., Brown, I., Harder, T., Stegeman, A., Abolnik, C., Delgado, M., Awada, L., Pavade, G., & Torres, G. (2024). Strategic challenges in the global control of high pathogenicity avian influenza. *Revue Scientifique Et Technique*, *Special Edition*, 89–102. https://doi.org/10.20506/rst.SE.3563

Székely, T. (2019). Why study plovers? The significance of non-model organisms in avian ecology, behaviour and evolution. *Journal of Ornithology*, *160*(3), 923–933. https://doi.org/10.1007/s10336-019-01669-4

Thompson, B. C., Jackson, J. A., Burger, J., Hill, L. A., Kirsch, E. M., & Atwood, J. L. (2020). Least Tern (Sternula antillarum), version 1.0. *Birds of the World*. https://doi.org/10.2173/bow.leater1.01

Toland, B. (1999). Nest Site Characteristics, Breeding Phenology, and Nesting Success of American Oystercatchers in Indian River County, Florida. *Florida Field Naturalist*, *27*(3), 112–116. https://digitalcommons.usf.edu/ffn/vol27/iss3/5

US Fish and Wildlife Service. (2026). *Species | U.S. Fish & Wildlife Service*. https://www.fws.gov/species

van de Pol, M., Bailey, L. D., Frauendorf, M., Allen, A. M., van der Sluijs, M., Hijner, N., Brouwer, L., de Kroon, H., Jongejans, E., & Ens, B. J. (2024). Sea-level rise causes shorebird population collapse before habitats drown. *Nature Climate Change*, *14*(8), 839–844. https://doi.org/10.1038/s41558-024-02051-w

van de Ven, T. M. F. N., McKechnie, A. E., & Cunningham, S. J. (2019). The costs of keeping cool: Behavioural trade-offs between foraging and thermoregulation are associated with significant mass losses in an arid-zone bird. *Oecologia*, *191*(1), 205–215. https://doi.org/10.1007/s00442-019-04486-x

van der Zande, A. N., ter Keurs, W. J., & van der Weijden, W. J. (1980). The impact of roads on the densities of four bird species in an open field habitat—Evidence of a long-distance effect. *Biological Conservation*, *18*(4), 299–321. https://doi.org/10.1016/0006-3207(80)90006-3

Virzi, T. (2010). The effect of human disturbance on the local distribution of American oystercatchers breeding on barrier island beaches. *Wader Study Group Bulletin*, *117*(1), 19–26. https://www.waderstudygroup.org/article/2144/

Virzi, T., Lockwood, J. L., Drake, D., Grodsky, S. M., & Pover, T. (2016). Conservation implications of reproductive success of American Oystercatchers in an urbanized barrier Island complex. *Wader Study*, *123*(3), 202–212. https://doi.org/10.18194/ws.00049

Walker, K. M. (2020). *Piping Plover (Charadrius melodus) habitat selection, survival, and migration on New York barrier islands following natural and engineered habitat changes* [Master's Thesis, Virginia Tech]. http://hdl.handle.net/10919/97889

Walker, K. M., Fraser, J. D., Catlin, D. H., Ritter, S. J., Robinson, S. G., Bellman, H. A., DeRose-Wilson, A., Karpanty, S. M., & Papa, S. T. (2019). Hurricane Sandy and engineered response created habitat for a threatened shorebird. *Ecosphere*, *10*(6), e02771. https://doi.org/10.1002/ecs2.2771

Warnock, N., Jennings, S., Kelly, J. P., Condeso, T. E., & Lumpkin, D. (2021). Declining wintering shorebird populations at a temperate estuary in California: A 30-year perspective. *Ornithological Applications*, *123*(1), duaa060. https://doi.org/10.1093/ornithapp/duaa060

Wei, E. A., Miselis, J. L., & Forde, A. S. (2021). Shoreface and Holocene sediment thickness offshore of Rockaway Peninsula, New York. In *Open-File Report* (Nos. 2021–1100; pp. 1–14). U.S. Geological Survey. https://doi.org/10.3133/ofr20211100

Wei, E., & Miselis, J. (2022). Geologic Framework, Anthropogenic Impacts, and Hydrodynamics Contribute to Variable Sediment Availability and Shoreface Morphology at the Rockaway Peninsula, NY. *Journal of Marine Science and Engineering*, *10*(989), 1–26. https://doi.org/10.3390/jmse10070989

Weiser, E. L., Brown, S. C., Lanctot, R. B., Gates, H. R., Abraham, K. F., Bentzen, R. L., Bêty, J., Boldenow, M. L., Brook, R. W., Donnelly, T. F., English, W. B., Flemming, S. A., Franks, S. E., Gilchrist, H.

G., Giroux, M.-A., Johnson, A., Kendall, S., Kennedy, L. V., Koloski, L., … Sandercock, B. K. (2018). Effects of environmental conditions on reproductive effort and nest success of Arctic-breeding shorebirds. *Ibis*, *160*(3), 608–623. https://doi.org/10.1111/ibi.12571

White, H. (1980). A Heteroskedasticity-Consistent Covariance Matrix Estimator and a Direct Test for Heteroskedasticity. *Econometrica*, *48*(4), 817–838. https://doi.org/10.2307/1912934

Wiggins, D., Morris, R., Nisbet, I., & Custer, T. (1984). Occurrence and Timing of Second Clutches in Common Terns. *The Auk*, *101*(2), 281–287. https://digitalcommons.usf.edu/auk/vol101/iss2/8

Wiltermuth, M. T., Anteau, M. J., Sherfy, M. H., & Shaffer, T. L. (2009). Nest Movement by Piping Plovers in Response to Changing Habitat Conditions. *The Condor: Ornithological Applications*, *111*(3), 550–555. https://doi.org/10.1525/cond.2009.080106

Wood, S. N. (2017). *Generalized Additive Models: An Introduction with R* (2nd ed.). Chapman and Hall/CRC. https://doi.org/10.1201/9781315370279

Working Group, A. O., Nol, E., & Humphrey, R. C. (2020). American Oystercatcher (Haematopus palliatus), version 1.0. *Birds of the World*. https://doi.org/10.2173/bow.ameoys.01

Zeigler, S. L., Gutierrez, B. T., Hecht, A., Plant, N. G., & Sturdivant, E. J. (2021). Piping plovers demonstrate regional differences in nesting habitat selection patterns along the U.S. Atlantic coast. *Ecosphere*, *12*(3), e03418. https://doi.org/10.1002/ecs2.3418

Zeigler, S. L., Gutierrez, B. T., Sturdivant, E. J., Catlin, D. H., Fraser, J. D., Hecht, A., Karpanty, S. M., Plant, N. G., & Thieler, E. R. (2019). Using a Bayesian network to understand the importance of coastal storms and undeveloped landscapes for the creation and maintenance of early successional habitat. *PLOS ONE*, *14*(7), e0209986. https://doi.org/10.1371/journal.pone.0209986