

Article

Shorebird Monitoring Using Spatially Explicit Occupancy and Abundance

Eve Bohnett ^{1,2,*} , Jessica Schulz ³, Robert Dobbs ⁴, Thomas Hootor ^{2,5}, Dave Hulse ^{2,6}, Bilal Ahmad ⁷ , Wajid Rashid ⁸  and Hardin Waddle ¹

¹ U.S. Geological Survey, Gainesville, FL 32601, USA

² Department of Landscape Architecture, University of Florida, Gainesville, FL 32601, USA

³ New Hampshire Department of Environmental Services, Concord, NH 03301, USA

⁴ Wildlife Diversity Program, Louisiana Department of Wildlife and Fisheries, Lafayette, CA 70506, USA

⁵ Center for Landscape Conservation Planning, University of Florida, Gainesville, FL 32601, USA

⁶ Florida Institute for Built Environment Resilience, University of Florida, Gainesville, FL 32601, USA

⁷ Institute of Agriculture Sciences and Forestry, University of Swat, Mingora 19130, Pakistan

⁸ Department of Environmental and Conservation Sciences, University of Swat, Mingora 19130, Pakistan

* Correspondence: evebohnnett@yahoo.com

Abstract: Loss of habitat and human disturbance are major factors in the worldwide decline of shorebird populations, including that of the threatened migratory piping plover (*Charadrius melodus*). From 2013 to 2018, we conducted land-based surveys of the shorebird community every other week during the peak piping plover season (September to March). We assessed the ability of a thin plate spline occupancy model to identify hotspot locations on Whiskey Island, Louisiana, for the piping plover and four additional shorebird species (Wilson's plover (*Charadrius wilsonia*), snowy plover (*Charadrius nivosus*), American oystercatcher (*Haematopus palliatus*), and red knot (*Calidris canutus*)). By fitting single-species occupancy models with geographic thin plate spline parameters, hotspot priority regions for conserving piping plovers and the multispecies shorebird assemblage were identified on the island. The occupancy environmental covariate, distance to the coastline, was weakly fitting, where the spatially explicit models were heavily dependent on the spatial spline parameter for distribution estimation. Additionally, the detectability parameters for Julian date and tide stage affected model estimations, resulting in seemingly inflated estimates compared to assuming perfect detection. The models predicted species distributions, biodiversity, high-use habitats for conservation, and multispecies conservation areas using a thin-plate spline for spatially explicit estimation without significant landscape variables, demonstrating the applicability of this modeling approach for defining areas on a landscape that are more heavily used by a species or multiple species.

Keywords: piping plover; thin plate spline; occupancy model; migratory shorebirds; multispecies occupancy; *N*-mixture models



Citation: Bohnett, E.; Schulz, J.; Dobbs, R.; Hootor, T.; Hulse, D.; Ahmad, B.; Rashid, W.; Waddle, H. Shorebird Monitoring Using Spatially Explicit Occupancy and Abundance. *Land* **2023**, *12*, 863. <https://doi.org/10.3390/land12040863>

Academic Editor: Alejandro Javier Rescia Perazzo

Received: 18 February 2023

Revised: 4 April 2023

Accepted: 8 April 2023

Published: 11 April 2023



Copyright: © 2023 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

1. Introduction

Throughout their annual cycle, migratory shorebirds depend on multiple geographic locations, making them vulnerable to the loss and degradation of habitat at critical points along their migration routes, which can endanger an entire species' population [1,2]. Implications of large-scale global changes threatening migratory bird habitats, such as climate, land use, or land cover change, necessitate understanding local, fine-scale species distributions and habitat use to guide conservation efforts [3]. Using species distribution models (SDM), ecologists frequently investigate migratory bird distributions to comprehend localized hotspot distributions for single and multiple species. Identifying highly visited areas is necessary for defining critical habitats and microhabitats for migratory birds [4], where identifying umbrella species can result in cascading conservation benefits for other species [5].

Multiple species occupying similar niches or utilizing similar habitats may benefit from a management strategy focusing on umbrella species, given that ecologically similar species frequently face similar threats and experience similar ecological factors. SDMs for migratory birds, such as the piping plover (*Charadrius melodus*), provide essential decision support for environmental managers in identifying suitable sites for prioritizing conservation protections. However, SDMs also incur contentious uncertainties and biases, such as those due to spatial autocorrelation from species detections being clustered or from imperfectly detecting the animals, which can impact the accuracy of estimates [6]. Therefore, it is crucial to visualize and understand umbrella species and the potential benefits of protection for other species by administering the SDMs with appropriate statistical modeling techniques such as occupancy and *N*-mixture modeling.

To model species distributions in a way that accounts for spatial autocorrelation and imperfect detection, modifications have been made to the occupancy and *N*-mixture modeling framework [7–9]. Autocorrelation, or clustering, in residuals can be observed in species distributions when significant population processes such as animal behavior that causes aggregations (such as roosting, colonial behavior, and foraging in groups), movement (such as migratory behavior), or when spatially autocorrelated resources or other environmental variables (e.g., sea surface temperature) are present [10,11]. Autocorrelation issues can confound statistical analysis, as the model residuals can no longer be treated as independent [12]. Overestimating the accuracy of occupancy and abundance estimates can also occur if spatial autocorrelation is ignored. Autocorrelation causes predictions of species distribution across the landscape to be spatially disaggregated, noisy, and devoid of species hotspots [8].

Numerous techniques have been developed to eliminate autocorrelation and improve statistical inferences by incorporating spatial terms that represent neighborhood locational effects [13–17]. Autologistic terms, which account for the effects of having neighboring grid cells populated with the focal species using neighborhood weights matrices, are the most prevalent method of incorporating spatial considerations into an occupancy modeling framework [9,18,19]. Studies of multispecies occupancy models have previously attempted to estimate species richness using autocovariate terms to account for spatial autocorrelation [20,21] or conditional autoregressive terms [22].

Recently, the use of basis functions (such as splines) to comprehend complex nonlinearities in spatiotemporal ecological relationships has been developed to address spatial autocorrelation [15]. Semiparametric modeling techniques, such as generalized additive models (GAM), employ thin-plate splines to generate a basis expansion on the distances between spatial grid cells and knots placed over the study area to generate a smoothing matrix comparable to a GAM smooth that can account for the random effects of spatial autocorrelation between locations [15,23–25]. Splines are used extensively for covariates and placement in models in ecological research. In contrast to parametric models, where the model predetermines the shape of the functional relationship between the response and predictors, the data determines the shape in nonparametric models [26]. One study used penalized splines to smooth out data from capture–recapture models of snow petrels, allowing the researchers to find nonlinear sex and climatic effects on species distributions [27]. Using a geospatial semiparametric linear model, a study discovered spatially explicit relationships for the distributions of individual species of warblers, such as patch size and landscape composition [28]. In another study, researchers modeled swift parrot distributions within an occupancy-based GAM-like zero-inflated binomial model with covariates such as flower distributions and a spatial smooth to account for imperfect detection [19]. Using a low-rank thin-plate spline on logistic regressions (occupancy) for spatial terms in the occupancy model can reveal spatial structures that would otherwise remain undetected when using conventional methods and covariates. With the addition of these spline terms, spatial autocorrelation problems in model residuals have been resolved [8,19,24].

Using point count data aggregated to a predefined continuous grid; we analyzed the spatial distributions of piping plover concentrations and shorebird diversity across

Whiskey Island in the barrier islands of Louisiana. We applied a Bayesian single-species (piping plover) single-season occupancy model with thin-plate splines on the spatial knots to account for spatial autocorrelation and provide spatially explicit results. Models assuming perfect detectability ($p = 1$) and models with occupancy covariates for distance to the shoreline were also compared with those including detectability covariates for Julian date and tide stage. We also applied splines to a single-season multispecies occupancy, further illustrating the value of occupancy modeling for multiple species. To investigate umbrella effects, we conducted several analyses to determine whether piping plovers and other shorebird species share common habitats. To pinpoint the spatial distribution of overlapping species groups, we evaluated the benefits and drawbacks of employing spatial spline terms in multispecies occupancy models to determine hotspots of species richness from detailed point counts.

2. Materials and Methods

2.1. Study Area

Data collection was conducted on Whiskey Island (90.84° W, 29.03° N), an island within the Isles Dernieres chain of barrier islands off the coast of Louisiana (Figure 1). The island consists of approximately 4.65 miles of beach and dune habitats on its southern (Gulf of Mexico)-facing shoreline, with overwash areas, unvegetated sand flats, meadow habitats, and salt marsh/mangroves on its northern (bay) side. Whiskey Island and the rest of the Isles Dernieres have experienced dramatic land loss in recent decades due to erosion, storms, and other factors, especially to intertidal and beach areas [29,30].



Figure 1. Whiskey Island, Louisiana, and locations of migratory bird observations.

Several major disturbances occurred during the data collection time frame. From 2017 to 2018, over 10 million cubic yards of sand were pumped from an offshore borrow source onto the Gulf side of the island to increase the area and elevation of beach and dune habitats, as well as onto the western portion of the bay side of the island to restore marsh habitat [31]. This dramatically expanded the unvegetated habitat available for use by target species. Tropical storms Bill and Cindy impacted the island in June 2015 and June 2017, respectively, producing winds of 35–45 knots and storm surges approximating 0.67 m (Bill) and 0.59 m (Cindy) on Whiskey Island [32,33]. Tropical storm Cindy in particular contributed to short-term declines in breeding bird use of the island [34,35].

2.2. Study Species

In the study area, the occupancy of piping plover (*Charadrius melodus*) and other resident and migratory species (Wilson's plover (*Charadrius wilsonia*), snowy plover (*Charadrius nivosus*), American oystercatcher (*Haematopus palliatus*), and red knot (*Calidris canutus*) were assessed. Among these species, piping plovers have garnered the most conservation concern, with declining populations shown from long-term census data [36], the breeding populations in the U.S. Great Plains and Atlantic coast are listed as threatened, while the breeding population in the Great Lakes is listed as endangered; all populations are categorized as threatened on their wintering grounds (e.g., coastal Louisiana) [37,38]. Although breeding populations of piping plovers are isolated geographically and separated by great distances, the population may be connected through shared nonbreeding wintering habitats. Piping plovers spend approximately ten months (July through May) migrating and wintering. Each overwintering location plays a role in the long-term viability of specific breeding populations [39].

Studies indicate that most piping plovers on the Gulf coast originate from the Great Lakes/Northern Great Plains breeding population, with over half of the population spending the winter in Texas. Breeding populations from the Great Lakes and Great Plains have dispersed to numerous coastal locations, preferring intertidal zones with productive benthic invertebrate prey bases [40], and showing site fidelity to their wintering areas, staying relatively in the same areas for the season [41]. However, fewer researchers have focused on Louisiana and South Carolina because of the states' smaller overwintering populations [41,42]. Since the overwintering grounds of the piping plover are not well managed for recovery, there is an increased need for fine-scale habitat use for targeted conservation.

The common overwintering grounds of these birds can become highly disturbed, especially during extreme environmental disturbances such as hurricanes or harmful algal blooms, affecting the nonbreeding survival of piping plovers [43]. Important factors influencing beach habitat on the wintering grounds of migratory shorebirds, such as the piping plover, include sea level rise, habitat loss due to land conversion for beach development and recreation, and coastal engineering activities such as channelization, sea walls, and riprap (hard structures) for shoreline stabilization. These factors may result in a decline in local abundance or extirpation due to diminished habitat suitability and habitat quality [44].

Numerous shorebirds of various species typically occupy wintering habitats. In wintering areas where populations have gradually declined due to land conversions and degradations, the community composition is determined by the quality of the habitat. Additional coastal protections along a substantial portion of the range of the piping plover would have a multiplicative effect on the conservation of a wide variety of shorebird species [5,41].

2.3. Data Collection

Data collection was standardized and carried out per U.S. Geological Survey (USGS) protocols. Surveyors (two per survey, working independently) employed an area search protocol, and covered all suitable shorebird habitat by foot on all surveys, ensuring consistent coverage of the island throughout the survey period [35]. This protocol allowed observers to maximize detections by limiting the need to search more than 100 m on either side of a survey track. Surveyors collected fine-scale data for all focal shorebird species, including exact latitude–longitude coordinates (using global positioning system units) for the locations of all individual birds detected. Surveys were conducted biweekly during all seasons year-round (2013–2018).

Surveys yielded 1103 observations of five species (piping plover, Wilson's plover, snowy plover, American oystercatcher, and red knot) (Table 1). A 50 m² grid was superimposed on the study area and subset to the dimensions of Whiskey Island and the range of bird distributions, resulting in 1690 grid cells covering the island (Table 2). Information collected by observers and researchers included the species, behavior, and tide stage.

Table 1. Summary of shorebird observations showing the total number of birds sighted for total detections.

Species	Total Detections	Year1	Year2	Year3	Year4	Year5
American oystercatcher	40	-	16	7	10	7
Piping plover	526	57	117	112	123	117
Red knot	40	-	4	7	4	25
Snowy plover	210	-	26	53	67	62
Wilson's plover	408	-	116	111	91	81

Table 2. Summary of shorebird observations showing the total number of occupied grid cells when transformed into a binary (0/1) matrix.

Species	Total Detections	Year1	Year2	Year3	Year4	Year5
American oystercatcher	16	-	2	4	7	3
Piping plover	325	41	70	87	53	74
Red knot	22	-	2	5	3	12
Snowy plover	121	-	17	37	27	38
Wilson's plover	72	-	13	25	18	12

The data were then collated into grid cells and transformed into presence/absence data for analysis in an occupancy framework, separately for each survey year (Table 2). The data were subset between September and March, the most common period for shorebird migration surveys. During this timeframe, at least 14 surveys per year were conducted on the island (2013–2018). Some species have a more clustered behavior, such as the Wilson's plover, which occupied a much smaller portion of the island's overall grid when converted to binary observations.

2.4. Data Analysis

Occupancy monitoring is ascertaining the likelihood that a site is occupied by collecting and analyzing data from a series of presence–absence surveys conducted at a random subset of locations across the study area [45]. Two distinct logistic regression procedures—one to account for differences in occupancy levels between sites and another to account for data on detection and non-detection at individual sites—form the basis of the model [24]. Occupancy models incorporate one model for species occurrence and imperfect detection (Equations (1) and (2)), to which covariate information may be added. Occupancy models are less expensive and more practical than abundance estimations and can help understand habitat use and management. To estimate occupancy for a single species, we used a Bayesian hierarchical parameterization of the model [46,47].

State process (occurrence):

$$z_i \sim \text{Bernoulli}(\psi_i) \quad (1)$$

Observation process (detection):

$$y_{ij}|z_i \sim \text{Bernoulli}(z_i p_{ij}) \quad (2)$$

The models were parameterized at each site (i) and for each repeated survey (j). The model assumes independent parameters with marginally informative prior distributions.

Furthermore, occupancy models can use presence–absence data for multiple species linked together to yield species richness estimates [48–50], enabling multispecies decision-making [51,52]. For a community-level analysis of species occurrence data, we extended the single-species model to a multispecies framework, where hierarchical models include a data table for each species and a detectability model to account for imperfect detection.

Hence, the model estimates each species in concert with others (Equations (3) and (4)) [53]. Hierarchical community models include a super-community with nested species occurrences [49]. Imperfect detection errors can skew parameter estimations and cause the true occurrence probability to be underestimated. MSOM models aim to increase our knowledge of a species' community, geographic distribution, and potential relationships to environmental covariates [50].

State process (occurrence):

$$z_{ik} \sim \text{Bernoulli}(\psi_{ik}) \quad (3)$$

Observation process (detection):

$$y_{ijk} | z_{ik} \sim \text{Bernoulli}(z_{ik} p_{ijk}) \quad (4)$$

The models were parameterized for each species (k), at each site (i), and for multiple repeated surveys (j).

N -mixture models have been used for estimating population abundances considering imperfect detection at spatially and temporally repeated avian count surveys [54]. These models were extended with underlying Poisson, negative binomial, or zero-inflated Poisson distributions that would allow for demographic stochasticity in birth and death processes [55]. The N -mixture model extends the Poisson GLM [56].

Models were tailored to the sampling site's environmental heterogeneity by including abundance and detectability covariates within the hierarchical modeling framework (Equations (5) and (6)) [57,58]. Note that N -mixture models are strongly affected by heterogeneity and nonindependence of detection [59].

State process:

$$N_i \sim \text{Poisson}(\lambda) \quad (5)$$

Observation process:

$$y_{ij} | N_i \sim \text{Binomial}(N_i, p_{ij}) \quad (6)$$

Occupancy and N -mixture models can incorporate imperfect detection of any potential false absences during the survey [46,54]. Bird distributions are considered imperfectly detected when available at a location but not present during the survey or unheard or unseen during the surveys [21,60]. For comparison, the detectability of the species can be considered "perfect" and set to equal one without any covariates to model perfect detectability [19]. Detection probability ($p_{i,j,k}$) uses α_k to parameterize both the Julian date and tide stage, to understand effects on species detectability (Equation (7)). Otherwise, detection probability was set to 1 for comparison to models with perfect detection (Equation (8)).

Observation process (detection):

With detection effects

$$\sim \alpha_0 + \alpha_1 * \text{date}_{ij} + \alpha_2 * \text{date}_{ij}^2 + \alpha_3 * \text{Tide Stage}_{ij} \quad (7)$$

With perfect detection

$$\sim 1 \quad (8)$$

Occupancy and N -mixture models assume a parametric structure. The parametric approach is flexible, where the covariates' polynomials and various nonlinear functions are parametric, achieving well-fitted models [24,61]. Although very efficient, the parametric approach can be limiting for modeling new data and is easily parameterized incorrectly, such as in the case of issues with spatial autocorrelation. Therefore, nonparametric and semiparametric approaches such as splines offer flexibility. Logistic and Poisson regressions can be fit with splines on one or all the predictors, which allows for the use of knots to fit the predictors at various lengths of the function. Multiple modeling methods that account

for spatial autocorrelation, including basis splines, conditional autoregressive models, and autologistic models, can be used to consider spatial dependence in ecological datasets when solving inferential problems [12,62,63]. To account for the nonlinear nature of environmental variability and spatial dependencies, spline terms analogous to GAM smooths have been incorporated into spatially explicit occupancy and N -mixture modeling. The study area is covered with a predetermined grid, then divided into knots. Each knot section's data is fitted independently, adding knot functions to predict the link function. This presupposes that the components are smooth and that the functions are additive. To deal with spatial autocorrelation problems and to perform spatially explicit approximations of species distribution, the incorporation of spline smooth terms into occupancy and N -mixture models has been developing slowly. Fitting a spatial spline as a covariate in the model can lead to better model fitting and more accurate spatial predictions (Equations (9) and (10)).

State process:

With thin-plate spline:

$$\sim \beta_0 + \sum_{R=1}^R b_r q_{i,r} \quad (9)$$

With occupancy covariates for distance to shoreline and thin-plate spline:

$$\sim \beta_0 + \beta_1 * \text{distance to shoreline} + \sum_{R=1}^R b_r q_{i,r} \quad (10)$$

where β_0 is the intercept term. Betas on the spline term (b_r) were represented along each knot of the spatial surface r . q_{ir} is the (i,r) th entry of the design matrix $Q = Q_r \Omega_r^{1/2}$ corresponding to random effects site occupancy for the spline function's penalized spline coefficients (b_r) [64]. Spatial knots were generated based on the multiscale grid sizes used for the analysis. Knots and random effects were generated with functions from the AHMBook package [24].

All occupancy and N -mixture models with and without spatial terms were fit in a Bayesian framework using jagsUI [65] in program R [66]. We used noninformative priors and ran three chains for 8000 iterations, burning 1000 and thinning 100. The convergence of the models was assessed by having an R-hat of <1.1.

2.5. Model Evaluation

Model performance was assessed by computing a Bayesian posterior predictive check to assess Bayesian p -values [67]. Bayesian p -values can check the observed against simulated data with values closer to 0.5, indicating the proper fit. The p -values determine whether the model's data-generating process could reconstruct the original dataset. All models indicated a proper fit with values very close to 0.5. Spatial autocorrelation was also assessed for each of the model's residuals. To compute the residuals of the models, the DHARMA package [68] used the simulations in the Bayesian models and the observed data. Then, spatial autocorrelation was assessed using Moran's I and correlograms for each year of the surveys separately and compared across the different models. The results of running Moran's I on the model residuals for each of the four models (null, spline with perfect detection, spline with occupancy, and detection covariates), showed that there was no significant spatial autocorrelation for any residuals, indicating satisfaction of assumptions for the independence of model residuals.

3. Results

Our analysis comprised single species (Figure 2) and multispecies occupancy (Figure 3) outputs and mapping. Details of the distributions of plovers and the multispecies shorebirds reveal the overlap between the two. The occupancy (ψ) of the piping plover and the number of sites occupied by the piping plover varied between models (Table 3). These results varied considerably between the null, spline with detection, and spline assuming perfect detection = 1. All the estimates for occupancy and the number of sites occupied var-

ied between years, although the spatial distribution appeared to be similar between years. Posterior predictive checks for Bayesian p -value revealed the null, spline with detection covariates, and spline with detection = 1; this model fit very well for every year (~ 0.50).

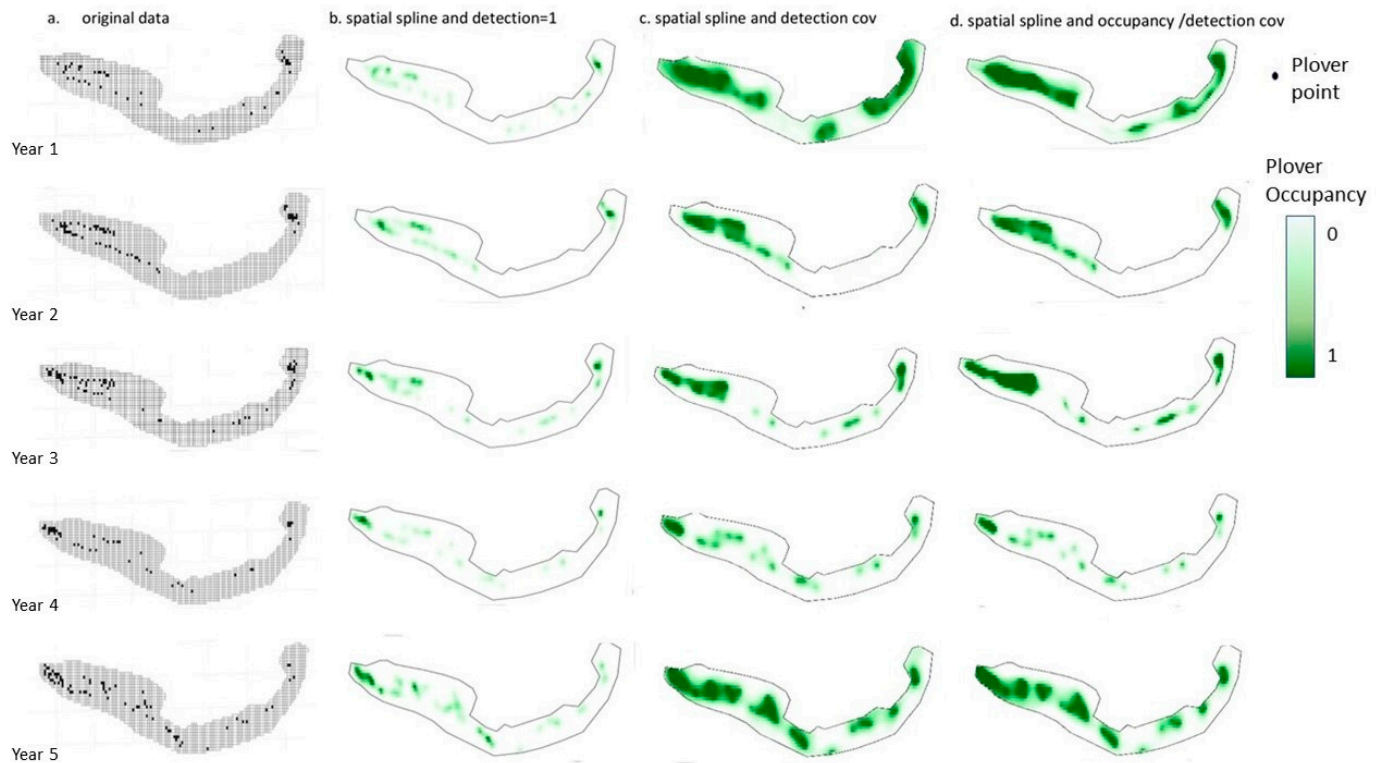


Figure 2. Piping plover occupancy with the spatial spline maps of hotspot distribution areas, showing areas with perfect detection (1), areas with detection covariates, and occupancy/detection covariates. For visual comparison, the original data are provided. Values range from 0 (white) to 1 (dark green).

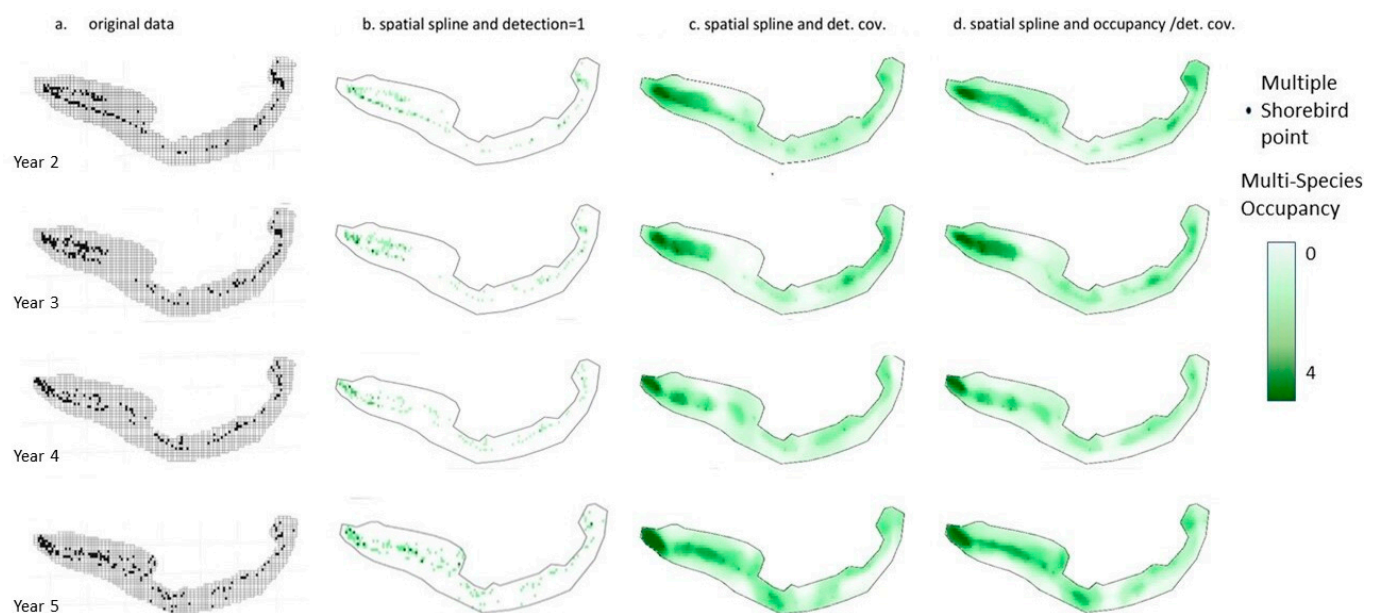


Figure 3. Species richness maps with the spatial spline for the island's four other migratory bird species (Wilson's plover, American oystercatcher, snowy plover, and red knot). Values range from 0 (white) to 4 (dark green).

Table 3. Piping plover model estimates for occupancy, reporting the mean and 97.5% confidence interval (CI) for each of the four models across the five years.

Year	Null Model		Spline with Detection = 1		Spline with Detection Covariates		Spline with Occupancy and Detection Covariates	
	Mean	(2.5%, 97.5%)	Mean	(2.5%, 97.5%)	Mean	(2.5%, 97.5%)	Mean	(2.5%, 97.5%)
1	0.071	(0.039, 0.130)	0.026	(0.002, 0.109)	0.424	(0.075, 0.915)	0.323	(0.096, 0.736)
2	0.066	(0.050, 0.091)	0.039	(0.006, 0.121)	0.160	(0.024, 0.377)	0.148	(0.019, 0.329)
3	0.081	(0.059, 0.115)	0.042	(0.007, 0.130)	0.155	(0.032, 0.376)	0.167	(0.076, 0.346)
4	0.053	(0.034, 0.083)	0.028	(0.004, 0.104)	0.122	(0.013, 0.442)	0.077	(0.011, 0.272)
5	0.142	(0.086, 0.243)	0.044	(0.005, 0.151)	0.341	(0.071, 0.795)	0.300	(0.062, 0.672)
Number of occupied grid cells (out of 1690 grid cells across the island) for single species plover occupancy models for each of the five years of the survey, reporting the mean and 97.5% confidence interval (CI).								
1	121	(72, 213)	41	(41, 41)	717	(489, 853)	546	(397, 760)
2	112	(87, 146)	63	(63, 63)	268	(143, 360)	250	(119, 339)
3	140	(106, 184)	70	(70, 70)	261	(161, 341)	282	(232, 329)
4	89	(65, 131)	46	(46, 46)	205	(90, 373)	129	(79, 218)
5	240	(155, 410)	72	(72, 72)	574	(434, 746)	507	(377, 645)

The results from *N*-mixture models resulted in estimates for abundance (*N*) and total abundance (total *N*) for the four models (null, spline with perfect detection, spline with detection covariates, spline with occupancy, and detection covariates), as well as predictive mapping (Figure 4, Table 4). These estimates reveal the impact of adding detection covariates to the model as the spline models with detection covariates are highly sensitive to Julian date and tide stage. Some estimates for the island's total *N* appear to be unrealistic.

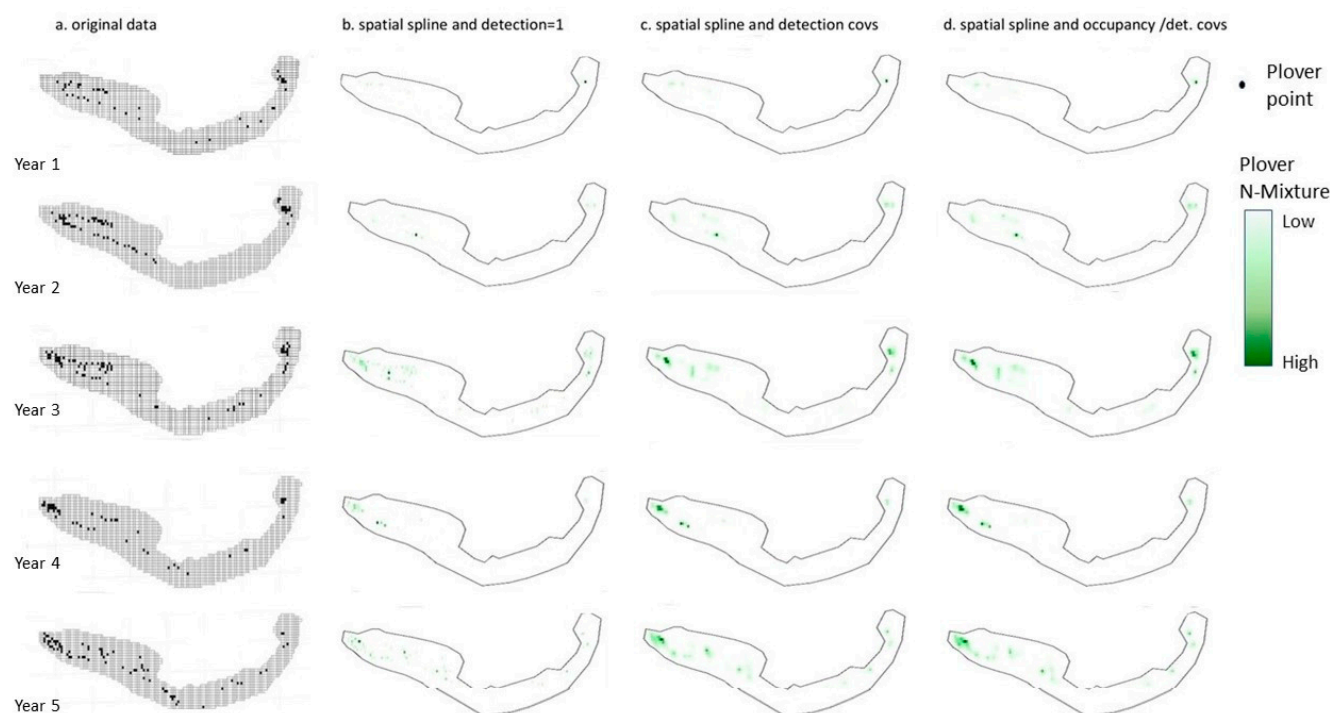


Figure 4. Piping plover *N*-mixture model with the spatial spline maps of hotspot distribution areas. Values range from 0 (white) to the max values from Table 4 (dark green).

Table 4. Model estimates for piping plover total *N* for Whiskey Island, reporting the mean and 97.5% confidence interval (CI).

Year	Null Model		Spline with Detection = 1		Spline with Detection Covariates		Spline with Occupancy and Detection Covariates	
	Mean	(2.5%, 97.5%)	Mean	(2.5%, 97.5%)	Mean	(2.5%, 97.5%)	Mean	(2.5%, 97.5%)
1	294	(183, 469)	80	(80, 80)	19,531	(7938, 31,930)	10,820	(4924, 24,171)
2	376	(260, 528)	128	(128, 128)	27,857	(6949, 55,364)	16,619	(4821, 23,816)
3	262	(191, 349)	102	(102, 102)	13,413	(4314, 29,283)	10,817	(4733, 30,194)
4	428	(318, 575)	148	(148, 148)	46,662	(16,216, 80,486)	26,036	(11,788, 52,175)
5	508	(347, 784)	120	(120, 120)	8651	(4278, 14,533)	13,806	(4013, 22,503)
Estimates for <i>N</i> across grid cells for single species plover <i>N</i> -mixture models for each of the five years of the survey, reporting the mean and 97.5% confidence interval (CI).								
1	0.17	(0.05, 1.05)	0.05	(0.05, 0.05)	11.55	(1.86, 43.00)	6.4	(1.01, 26.73)
2	0.22	(0.08, 1.1)	0.08	(0.08, 0.08)	16.48	(2.22, 57.91)	9.83	(1.67, 29.32)
3	0.15	(0.06, 1.06)	0.06	(0.06, 0.06)	7.94	(1.07, 29.82)	6.4	(0.91, 27.07)
4	0.25	(0.09, 1.14)	0.09	(0.09, 0.09)	27.61	(5.50, 85.39)	15.41	(3.86, 48.31)
5	0.3	(0.07, 1.41)	0.07	(0.07, 0.07)	5.12	(0.63, 18.95)	8.17	(0.92, 30.43)

4. Discussion

To aid in research and conservation efforts for multiple species, the results of this study provide critical quantitative baseline information on shorebird spatial patterns during peak migratory piping plover activity for nonbreeding sites within the Louisiana barrier islands. Many conservation actions have broader community-level shorebird distribution co-benefits, such as those critical habitats for endangered species such as the piping plover. We found that the piping plover's distribution closely matched the hotspots for species richness for occupancy of migratory shorebirds, indicating that this species preferred and did not appear to avoid areas that overlapped with high areas of species richness. Comparable findings were found in a previous study, where researchers used Maxent models to identify umbrella species along New Jersey's coast, finding that piping plovers' habitats overlap by 66 percent with American oystercatchers, least terns, and black skimmer birds [5]. Four additional migratory shorebirds were found to share a similar distributional pattern with piping plovers in our study. The conservation efforts for the piping plover will have downstream benefits for the numerous other species of shorebirds that use the same high-use hotspots, and this type of research can validate the concept of an umbrella species as applicable to downstream species protections and conservation benefits for a community of species sharing a habitat. An in-depth familiarity with the biological interactions between species and the environments they occupy is necessary for making conservation decisions for multiple species. The possible effects of conservation measures on the species of interest and others that may be impacted are additional considerations. Multispecies occupancy and abundance models can benefit conservation decision-making by providing a more complete and integrated approach to species management.

For single- and multispecies occupancy and *N*-mixture models, spatially explicit estimates for occupancy and abundance were derived using spatial thin-plate spline terms and defined hotspot areas. Due to the concentration of birds on the landscape, the spline terms resulted in specific occupancy estimates across grid cells, with definite hot spots of activity on certain portions of the island. On the other hand, the null model calculated island-wide occupancy and *N*-mixture estimates without identifying hotspots in the landscape, taking environmental heterogeneity into account, or predicting the effects of variability in detectability. The spline terms did help in visual comparison using plotted maps to identify areas of higher occupancy and abundance than other areas, showing very small, clustered areas on the landscape that were relatively similar between years. Without the spline term, the environmental covariates employed in our models were inadequately fitted and failed to identify locations with a higher degree of habitat specificity.

Detection covariates (tide stage, Julian date, Julian date²) influenced distribution estimates more than occupancy covariates (distance to shoreline). Estimates of occupancy, number of occupied grid cells, mean abundance across grid cells, and total abundance for the island all were significantly altered after the inclusion of detection covariates. However, occupancy/abundance covariates may also be more critical depending on the study, species, and habitat. The sensitivity selection of detection covariates is an important consideration for researchers implementing these spatially explicit models, as it had a much more significant effect on the numerical model outputs. In this study, we demonstrated that adding detectability covariates led to significantly different estimates for spatial spline models compared to both perfect detection ($p = 1$) and the inclusion of occupancy/abundance covariates. When perfect detection is assumed, the survey data are modeled to reflect the data without considering the possibility of variation throughout the rest of the season. Generally, we favor approaches that explicitly account for imperfect detection under a proper sampling design. The available data for this investigation were not intended for applying formal occupancy/ N -mixture models, which allow for imperfect detection within a subset sample, whereas we sampled the complete grid multiple times. Assuming perfect detection ($=1$) has the potential drawback of assuming that all birds that visit the island have been tallied perfectly, which is likely not the case for birds. However, we have a reasonable estimate of abundance where the spline model with perfect detection ($=1$) was close to the number surveyed and conservative compared to the null model or the models with imperfect detection.

However, if we applied parameters where detectability varied along with covariates (tide stage, Julian date, Julian date²), we noticed that one of the disadvantages of employing the N -mixture and occupancy models is inflated and unrealistic model estimates of the number of piping plovers or the number of grid cells occupied with variable imperfect detection. However, the hotspot maps from the N -mixture and occupancy models showed consistency spatially where the higher abundance or occupied pixels were found. A model estimate of these spatial factors would be expected to be displayed more strongly in the case of more pronounced abundance-related environmental factors. In our case, the spatial factors for environmental heterogeneity were weakly fitted, so the models heavily depended on the spline factor to estimate the spatial distribution of the species. All the spline models depicted areas of possibly greater abundance or occupancy on the maps, with the most conservative yearly estimates in the model with perfect detection ($=1$) and the models with varying detectability more loosely fitted. This does not account for heterogeneity and nonindependence of detection results in a bias in abundance estimates, consistent with previous research showing that detection probabilities estimated with N -mixture models are generally biased [69]. In our case, we attempted to account for this nonindependence of our spatial samples using the spline terms, which helped to differentiate areas on the landscape, thus resulting in a more conservative abundance estimate. Still, the covariates for detectability widely influenced the model estimates.

The limitations of this study included representing fine-scale habitat information for inclusion into occupancy/abundance covariates. We used a coarse scale distance to shoreline measurement as an environmental covariate for occupancy, which also served as the edge of the grid that overlaid the island. Since the island shoreline migrates annually due to sand movements and variable water heights, it was not easy to reconcile the GPS coordinates with the grid sizes of remote sensing data. Finer scale UAV or remote sensing basemap data for the entire island for each year would be necessary to accurately depict the available habitat, especially along the south shoreline, where there were regular island changes between years. Our analysis was successful in depicting general patterns, although even more exacting models that would perhaps render this covariate more significant are also possible.

Several improvements could be implemented for future monitoring. For example, to address the closure assumption within the secondary period, we could use two separate observers that would count the same plot over a short period of time (almost instantly);

alternatively, we could also use different sampling methods, such as human observations combined with UAS surveys. Improvements in understanding fine-scale habitat for the piping plover could be developed with sub-meter accurate GPS units and remote sensing.

5. Conclusions

We used occupancy models with spatial spline terms to pinpoint the most productive habitats for five species of shorebirds on Whiskey Island in Louisiana. Our results showed that piping plovers overlapped their use of these areas, indicating that these spots were particularly rich in biodiversity. Many species of shorebirds share habitats with piping plovers, thus providing cascading conservation benefits for their protection. This is the first study to apply spatial splines to the multispecies occupancy model and to gain a greater understanding of species that fall under the conservation umbrella of a focal species. Models that did not include the spatial thin-plate spline or occupancy covariates could not identify fine-scale distributions or distinct spatial patterns; instead, each grid cell yielded the same results when estimating the island-wide occupancy. We hope that our paper provides new insights into the benefits and limitations of using spatially explicit occupancy models (as well as *N*-mixture) for shorebird monitoring or other fine-scale monitoring data and possibly contributes to improving future shorebird monitoring program designs. The thin-plate spline revealed fine-scale hotspots of occupancy and abundance, which was particularly effective in the absence of strongly fitting environmental factors. The use of detectability covariates, which tended to inflate occupancy and abundance estimates, was identified as a drawback. However, these technologies enabled an approach for spatially explicit mapping that produced representations accurate enough to define meaningful distributions.

Author Contributions: Conceptualization: E.B. and H.W.; Data curation H.W.; Formal analysis E.B.; Funding acquisition H.W.; Investigation E.B.; Methodology E.B. and H.W.; Project administration H.W.; Resources J.S., H.W. and R.D.; Software E.B.; Supervision H.W., T.H. and D.H.; Validation; Visualization; Roles/Writing—original draft E.B.; Writing—review and editing E.B., J.S., R.D., B.A. and W.R. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Data Availability Statement: Data are available in Zenal et al. (2023) <https://doi.org/10.5066/P93MVS0S>.

Acknowledgments: Special thank you faculty at the University of Florida for engaging in commentary on this work. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Murray, N.J.; Marra, P.P.; Fuller, R.A.; Clemens, R.S.; Dhanjal-Adams, K.; Gosbell, K.B.; Hassell, C.J.; Iwamura, T.; Melville, D.; Minton, C.D.T.; et al. The Large-Scale Drivers of Population Declines in a Long-Distance Migratory Shorebird. *Ecography* **2018**, *41*, 867–876. [CrossRef]
2. Sutherland, W.J.; Alves, J.A.; Amano, T.; Chang, C.H.; Davidson, N.C.; Max Finlayson, C.; Gill, J.A.; Gill, R.E.; González, P.M.; Gunnarsson, T.G.; et al. A Horizon Scanning Assessment of Current and Potential Future Threats to Migratory Shorebirds. *Ibis* **2012**, *154*, 663–679. [CrossRef]
3. Zurell, D.; Graham, C.H.; Gallien, L.; Thuiller, W.; Zimmermann, N.E. Long-Distance Migratory Birds Threatened by Multiple Independent Risks from Global Change. *Nat. Clim. Chang.* **2018**, *8*, 992–996. [CrossRef] [PubMed]
4. Soanes, L.M.; Bright, J.A.; Angel, L.P.; Arnould, J.P.Y.; Bolton, M.; Berlincourt, M.; Lascelles, B.; Owen, E.; Simon-Bouhet, B.; Green, J.A. Defining Marine Important Bird Areas: Testing the Foraging Radius Approach. *Biol. Conserv.* **2016**, *196*, 69–79. [CrossRef]
5. Maslo, B.; Leu, K.; Faillace, C.; Weston, M.A.; Pover, T.; Schlacher, T.A. Selecting Umbrella Species for Conservation: A Test of Habitat Models and Niche Overlap for Beach-Nesting Birds. *Biol. Conserv.* **2016**, *203*, 233–242. [CrossRef]
6. Maslo, B.; Zeigler, S.L.; Drake, E.C.; Pover, T.; Plant, N.G. A Pragmatic Approach for Comparing Species Distribution Models to Increasing Confidence in Managing Piping Plover Habitat. *Conserv. Sci. Pract.* **2020**, *2*, e150. [CrossRef]
7. Chelgren, N.D.; Adams, M.J.; Bailey, L.L.; Bury, R.B. Using Multilevel Spatial Models to Understand Salamander Site Occupancy Patterns after Wildfire. *Ecology* **2011**, *92*, 408–421. [CrossRef]

8. Guélat, J.; Kéry, M. Effects of Spatial Autocorrelation and Imperfect Detection on Species Distribution Models. *Methods Ecol. Evol.* **2018**, *9*, 1614–1625. [\[CrossRef\]](#)
9. Poley, L.G.; Pond, B.A.; Schaefer, J.A.; Brown, G.S.; Ray, J.C.; Johnson, D.S. Occupancy Patterns of Large Mammals in the Far North of Ontario under Imperfect Detection and Spatial Autocorrelation. *J. Biogeogr.* **2014**, *41*, 122–132. [\[CrossRef\]](#)
10. Legendre, P. Spatial Autocorrelation: Trouble or New Paradigm? *Ecology* **1993**, *74*, 1659–1673. [\[CrossRef\]](#)
11. Legendre, P.; Fortin, M.J. Spatial Pattern and Ecological Analysis. *Vegetatio* **1989**, *80*, 107–138. [\[CrossRef\]](#)
12. Dormann, C.F.; McPherson, J.M.; Araújo, M.B.; Bivand, R.; Bolliger, J.; Carl, G.; Davies, R.G.; Hirzel, A.; Jetz, W.; Kissling, W.D.; et al. Methods to Account for Spatial Autocorrelation in the Analysis of Species Distributional Data: A Review. *Ecography* **2007**, *30*, 609–628. [\[CrossRef\]](#)
13. Besag, J. Spatial Interaction and the Statistical Analysis of Lattice Systems. *J. R. Stat. Soc. Ser. B (Methodol.)* **1974**, *36*, 192–225. [\[CrossRef\]](#)
14. Besag, J.E. Nearest-Neighbour Systems and the Auto-Logistic Model for Binary Data. *J. R. Stat. Soc. Ser. B (Methodol.)* **1972**, *34*, 75–83. [\[CrossRef\]](#)
15. Hefley, T.J.; Broms, K.M.; Brost, B.M.; Buderman, F.E.; Kay, S.L.; Scharf, H.R.; Tipton, J.R.; Williams, P.J.; Hooten, M.B. The Basis Function Approach for Modeling Autocorrelation in Ecological Data. *Ecology* **2017**, *98*, 632–646. [\[CrossRef\]](#)
16. Hoeting, J.A.; Leecaster, M.; Bowden, D. An Improved Model for Spatially Correlated Binary Responses. *J. Agric. Biol. Environ. Stat.* **2000**, *5*, 102. [\[CrossRef\]](#)
17. Wintle, B.A.; Bardos, D.C. Modeling Species-Habitat Relationships with Spatially Autocorrelated Observation Data. *Ecol. Appl.* **2006**, *16*, 1945–1958. [\[CrossRef\]](#)
18. Bardos, D.C.; Guillera-Arroita, G.; Wintle, B.A. Valid Auto-models for Spatially Autocorrelated Occupancy and Abundance Data. *Methods Ecol. Evol.* **2015**, *6*, 1137–1149. [\[CrossRef\]](#)
19. Webb, M.H.; Wotherspoon, S.; Stojanovic, D.; Heinsohn, R.; Cunningham, R.; Bell, P.; Terauds, A. Location Matters: Using Spatially Explicit Occupancy Models to Predict the Distribution of the Highly Mobile, Endangered Swift Parrot. *Biol. Conserv.* **2014**, *176*, 99–108. [\[CrossRef\]](#)
20. Burton, A.C.; Sam, M.K.; Balangtaa, C.; Brashares, J.S. Hierarchical Multi-Species Modeling of Carnivore Responses to Hunting, Habitat and Prey in a West African Protected Area. *PLoS ONE* **2012**, *7*, e38007. [\[CrossRef\]](#)
21. Mattsson, B.J.; Zipkin, E.F.; Gardner, B.; Blank, P.J.; Sauer, J.R.; Royle, J.A. Explaining Local-Scale Species Distributions: Relative Contributions of Spatial Autocorrelation and Landscape Heterogeneity for an Avian Assemblage. *PLoS ONE* **2013**, *8*, e55097. [\[CrossRef\]](#) [\[PubMed\]](#)
22. Carroll, C.; Johnson, D.S.; Dunk, J.R.; Zielinski, W.J. Hierarchical Bayesian Spatial Models for Multispecies Conservation Planning and Monitoring: Hierarchical Spatial Habitat Models. *Conserv. Biol.* **2010**, *24*, 1538–1548. [\[CrossRef\]](#) [\[PubMed\]](#)
23. James, G.; Witten, D.; Hastie, T.; Tibshirani, R. (Eds.) *An Introduction to Statistical Learning: With Applications in R*; Springer Texts in Statistics; Springer: New York, NY, USA, 2013; ISBN 978-1-4614-7137-0.
24. Kéry, M.; Royle, J.A. *Applied Hierarchical Modeling in Ecology: Analysis of Distribution, Abundance and Species Richness in R and BUGS: Volume 2: Dynamic and Advanced Models*; Elsevier Science: Amsterdam, The Netherlands, 2020; Volume 2.
25. Wood, S.N. *Generalized Additive Models: An Introduction with R*, 2nd ed.; Chapman & Hall/CRC: New York, NY, USA, 2017; ISBN 978-1-315-37027-9.
26. Crainiceanu, C.M.; Goldsmith, A.J. Bayesian Functional Data Analysis Using WinBUGS. *J. Stat. Soft.* **2010**, *32*, 1–33. [\[CrossRef\]](#)
27. Gimenez, O.; Crainiceanu, C.; Barbraud, C.; Jenouvrier, S.; Morgan, B.J.T. Semiparametric Regression in Capture-Recapture Modeling. *Biometrics* **2006**, *62*, 691–698. [\[CrossRef\]](#) [\[PubMed\]](#)
28. Collier, B.A.; Groce, J.E.; Morrison, M.L.; Newnam, J.C.; Campomizzi, A.J.; Farrell, S.L.; Mathewson, H.A.; Snelgrove, R.T.; Carroll, R.J.; Wilkins, R.N. Predicting Patch Occupancy in Fragmented Landscapes at the Rangeland Scale for an Endangered Species: An Example of an American Warbler: Occupancy Distribution of an American Warbler. *Divers. Distrib.* **2012**, *18*, 158–167. [\[CrossRef\]](#)
29. Kindinger, J.; Buster, N.; Flocks, J.; Bernier, J.; Kulp, M. *Louisiana Barrier Island Comprehensive Monitoring (BICM) Program Summary Report: Data and Analyses 2006 through 2010*; U.S. Department of the Interior U.S. Geological Survey: Tallahassee, FL, USA, 2013.
30. Enwright, N.; SooHoo, W.; Dugas, J.; Conzelmann, C.; Laurenzano, C.; Lee, D.; Mouton, K.; Stelly, S. *Louisiana Barrier Island Comprehensive Monitoring Program: Mapping Habitats in Beach, Dune, and Intertidal Environments Along the Louisiana Gulf of Mexico Shoreline, 2008 and 2015–16*; U.S. Department of the Interior U.S. Geological Survey: Tallahassee, FL, USA, 2020.
31. Coastal Engineering Consultants. *Louisiana Barrier Islands Restoration*; Coastal Engineering Consultants: Denham Springs, LA, USA, 2017.
32. Berg, R. *Tropical Storm Bill*; National Hurricane Center: Miami, FL, USA, 2015.
33. Berg, R. *Tropical Storm Cindy*; National Hurricane Center: Miami, FL, USA, 2018.
34. Zenal, T.J.; Anderson, A.N.; Geary, B.; Schulz, J.L.; Dobbs, R.C.; Barrow, W.C.; Waddle, J.H. *Early Season Tropical Storms Impact Birds Breeding on a Barrier Island*; U.S. Geological Survey: Tallahassee, FL, USA, 2023; *Unpublished (In Press)*.
35. Zenal, T.J.; Anderson, A.N.; Geary, B.J.; Schulz, J.; Dobbs, R.; Barrow, W.C.; Waddle, H. *Immediate Impacts of Tropical Storms on the Avian Breeding Community at Whiskey Island, Louisiana from 2015–2020*; U.S. Geological Survey: Tallahassee, FL, USA, 2022.
36. Haig, S.M.; Ferland, C.L. A Complete Species Census and Evidence for Regional Declines in Piping Plovers. *J. Wildl. Manag.* **2005**, *69*, 160–173. [\[CrossRef\]](#)

37. USFWS Endangered and Threatened Wildlife and Plants; Final Determinations of Critical Habitat for Wintering Piping Plovers; Final Rule. *Federal Register* **1985**, *50*, 50726–50734. Available online: https://archives.federalregister.gov/issue_slice/1985/12/11/50706-50724.pdf#page=15 (accessed on 25 May 2018).
38. USFWS Endangered and Threatened Wildlife and Plants; Final Determination of Critical Habitat for Wintering Piping Plovers 2001. Available online: <https://www.federalregister.gov/documents/2001/07/10/01-16905/endangered-and-threatened-wildlife-and-plants-final-determination-of-critical-habitat-for-wintering> (accessed on 21 May 2019).
39. Roche, E.A.; Cohen, J.B.; Catlin, D.H.; Amirault-Langlais, D.L.; Cuthbert, F.J.; Gratto-Trevor, C.L.; Felio, J.; Fraser, J.D. Range-Wide Piping Plover Survival: Correlated Patterns and Temporal Declines. *J. Wildl. Manag.* **2010**, *74*, 1784–1791. [\[CrossRef\]](#)
40. Schulz, J.L.; Leberg, P.L. Factors Affecting Prey Availability and Habitat Use of Nonbreeding Piping Plovers (*Charadrius melodus*) in Coastal Louisiana. *J. Coast. Res.* **2019**, *35*, 861. [\[CrossRef\]](#)
41. Gratto-Trevor, C.; Amirault-Langlais, D.; Catlin, D.; Cuthbert, F.; Fraser, J.; Maddock, S.; Roche, E.; Shaffer, F. Connectivity in Piping Plovers: Do Breeding Populations Have Distinct Winter Distributions? *J. Wildl. Manag.* **2012**, *76*, 348–355. [\[CrossRef\]](#)
42. Nicholls, J.; Baldassarre, G. Winter Distribution of Piping Plovers along the Atlantic and Gulf Coasts of the United States. *Wilson Bull.* **1990**, *102*, 400–412.
43. Ellis, K.S.; Anteau, M.J.; Cuthbert, F.J.; Gratto-Trevor, C.L.; Jorgensen, J.G.; Newstead, D.J.; Powell, L.A.; Ring, M.M.; Sherfy, M.H.; Swift, R.J.; et al. Impacts of Extreme Environmental Disturbances on Piping Plover Survival Are Partially Moderated by Migratory Connectivity. *Biol. Conserv.* **2021**, *264*, 109371. [\[CrossRef\]](#)
44. Zeigler, S.; Sturdivant, E.; Gutierrez, B. *Evaluating Barrier Island Characteristics and Piping Plover (Charadrius Melodus) Habitat Availability Along the U.S. Atlantic Coast—Geospatial Approaches and Methodology*; Open-File Report; USGS: Tallahassee, FL, USA, 2019. Available online: <https://pubs.usgs.gov/of/2019/1071/ofr20191071.pdf> (accessed on 20 May 2019).
45. MacKenzie, D.I.; Nichols, J.D.; Hines, J.E.; Knutson, M.G.; Franklin, A.B. Estimating Site Occupancy, Colonization, and Local Extinction When a Species Is Detected Imperfectly. *Ecology* **2003**, *84*, 2200–2207. [\[CrossRef\]](#)
46. MacKenzie, D.I.; Nichols, J.D.; Lachman, G.B.; Droege, S.; Andrew Royle, J.; Langtimm, C.A. Estimating Site Occupancy Rates When Detection Probabilities Are Less than One. *Ecology* **2002**, *83*, 2248–2255. [\[CrossRef\]](#)
47. An, L.; Bohnett, E.; Battle, C.; Dai, J.; Lewison, R.; Jankowski, P.; Carter, N.; Ghimire, D.; Dhakal, M.; Karki, J.; et al. Sex-Specific Habitat Suitability Modeling for Panthera Tigris in Chitwan National Park, Nepal: Broader Conservation Implications. *Sustainability* **2021**, *13*, 13885. [\[CrossRef\]](#)
48. Dorazio, R.M.; Royle, J.A. Estimating Size and Composition of Biological Communities by Modeling the Occurrence of Species. *J. Am. Stat. Assoc.* **2005**, *100*, 389–398. [\[CrossRef\]](#)
49. Bohnett, E.; Fandjinou, K.; Ahmad, B.; Mammo, S.; Hulse, D.; Hctor, T. Determining Community-Level Carnivore Response to Landscape Factors in Bukit Barisan Selatan National Park, Sumatra, Indonesia. *J. Wildl. Biodivers.* **2021**, *5*, 68–88. [\[CrossRef\]](#)
50. Bohnett, E.; Goossens, B.; Bakar, M.S.A.; Abidin, T.R.; Lim, H.-Y.; Hulse, D.; Ahmad, B.; Hctor, T.; Gardner, P. Examining Diversity of Terrestrial Mammal Communities across Forest Reserves in Sabah, Borneo. *Biodivers. Conserv.* **2022**, *31*, 1709–1734. [\[CrossRef\]](#)
51. Barker, N.K.S.; Slattery, S.M.; Darveau, M.; Cumming, S.G. Modeling Distribution and Abundance of Multiple Species: Different Pooling Strategies Produce Similar Results. *Ecosphere* **2014**, *5*, art158. [\[CrossRef\]](#)
52. Ferrier, S.; Guisan, A. Spatial Modelling of Biodiversity at the Community Level. *J. Appl. Ecol.* **2006**, *43*, 393–404. [\[CrossRef\]](#)
53. Zipkin, E.F.; DeWan, A.; Andrew Royle, J. Impacts of Forest Fragmentation on Species Richness: A Hierarchical Approach to Community Modelling. *J. Appl. Ecol.* **2009**, *46*, 815–822. [\[CrossRef\]](#)
54. Royle, J.A. N-Mixture Models for Estimating Population Size from Spatially Replicated Counts. *Biometrics* **2004**, *60*, 108–115. [\[CrossRef\]](#) [\[PubMed\]](#)
55. Joseph, L.N.; Elkin, C.; Martin, T.G.; Possingham, H.P. Modeling Abundance Using N-Mixture Models: The Importance of Considering Ecological Mechanisms. *Ecol. Appl.* **2009**, *19*, 631–642. [\[CrossRef\]](#) [\[PubMed\]](#)
56. Royle, J.A.; Kéry, M. *Applied Hierarchical Modeling in Ecology: Analysis of Distribution, Abundance and Species Richness in R and BUGS: Volume 1: Prelude and Static Models*; Elsevier Science & Technology: Amsterdam, The Netherlands, 2015.
57. Kéry, M. Estimating Abundance from Bird Counts: Binomial Mixture Models Uncover Complex Covariate Relationships. *The Auk* **2008**, *125*, 336–345. [\[CrossRef\]](#)
58. Kéry, M.; Royle, J.A.; Schmid, H. Modeling Avian Abundance from Replicated Counts Using Binomial Mixture Models. *Ecol. Appl.* **2005**, *15*, 1450–1461. [\[CrossRef\]](#)
59. Martin, J.; Royle, J.A.; Mackenzie, D.I.; Edwards, H.H.; Kéry, M.; Gardner, B. Accounting for Non-Independent Detection When Estimating Abundance of Organisms with a Bayesian Approach: Correlated Behaviour and Abundance. *Methods Ecol. Evol.* **2011**, *2*, 595–601. [\[CrossRef\]](#)
60. Mordecai, R.S.; Mattsson, B.J.; Tzilkowski, C.J.; Cooper, R.J. Addressing Challenges When Studying Mobile or Episodic Species: Hierarchical Bayes Estimation of Occupancy and Use: Hierarchical Bayes Multi-Scale Occupancy. *J. Appl. Ecol.* **2011**, *48*, 56–66. [\[CrossRef\]](#)
61. Faraway, J.J. *Extending the Linear Model with R*, 2nd ed.; Chapman & Hall/CRC: New York, NY, USA, 2016; ISBN 978-1-315-38272-2.
62. Beale, C.M.; Lennon, J.J.; Yearsley, J.M.; Brewer, M.J.; Elston, D.A. Regression Analysis of Spatial Data. *Ecol. Lett.* **2010**, *13*, 246–264. [\[CrossRef\]](#)

63. Levy, O.; Ball, B.A.; Bond-Lamberty, B.; Cheruvilil, K.S.; Finley, A.O.; Lottig, N.R.; Punyasena, S.W.; Xiao, J.; Zhou, J.; Buckley, L.B.; et al. Approaches to Advance Scientific Understanding of Macrosystems Ecology. *Front. Ecol. Environ.* **2014**, *12*, 15–23. [CrossRef]
64. Crainiceanu, C.; Ruppert, D.; Wand, M.P. Bayesian Analysis for Penalized Spline Regression Using WinBUGS. *J. Stat. Softw.* **2005**, *14*, 1–24. [CrossRef]
65. Kellner, K. Package “JagsUI” 2019.
66. R Core Team. *R: A Language and Environment for Statistical Computing*; R Core Team: Vienna, Austria, 2021.
67. Kéry, M. *Introduction to WinBUGS for Ecologists: A Bayesian Approach to Regression, ANOVA, Mixed Models and Related Analyses*, 1st ed.; Elsevier: Amsterdam, The Netherlands; Boston, MA, USA, 2010; ISBN 978-0-12-378605-0.
68. Hartig, F. DHARMA: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models. CRAN Repository 2022. Available online: <http://florianhartig.github.io/DHARMA/> (accessed on 1 May 2022).
69. Martin, J.; Sabatier, Q.; Gowan, T.A.; Giraud, C.; Gurarie, E.; Calleson, C.S.; Ortega-Ortiz, J.G.; Deutsch, C.J.; Rycyk, A.; Koslovsky, S.M. A Quantitative Framework for Investigating Risk of Deadly Collisions between Marine Wildlife and Boats. *Methods Ecol. Evol.* **2016**, *7*, 42–50. [CrossRef]

Disclaimer/Publisher’s Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.