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RESEARCH ARTICLE

Hydrologic variability and plant composition drive relative abundance of marsh birds at created and reference marshes in southeastern Louisiana, U.S.A.

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Coastal marsh loss occurs at an alarming pace globally, with extremely high rates along the northern Gulf of Mexico, particularly in Louisiana. In Louisiana, marsh creation projects combat wetland loss; however, biotic responses of vegetation and wildlife receive little to no consideration during and after construction. Habitat characteristics such as hydrologic processes, plant composition, and habitat structure affect the abundance of marsh birds, and understanding these features is important when creating suitable habitat for marsh birds. Our study compared hydrologic characteristics, plant composition, and habitat structure between created ($n = 10$) and reference ($n = 9$) sites across southeastern Louisiana and determined the relationship of these habitat characteristics to marsh bird relative abundance. We performed bird surveys ($n = 766$), including call-back surveys for secretive marsh birds, at all sites across three breeding seasons (2021–2023). We used drone imagery to determine plant composition and used water level recording devices to assess hydrologic characteristics. Our results indicate that hydrologic variation and plant composition are drivers of marsh bird relative abundance regardless of whether a marsh is created or not. While some habitat features differed between created and reference sites, our results indicated that created marshes can support similar abundances of marsh birds as reference sites, depending on what habitat features are present at the site. Our study demonstrates the importance of creating marshes that promote hydrologic connectivity and water level variability, which in turn supports diverse emergent vegetation communities and provides suitable habitat for a variety of marsh bird species.

Key words: coastal marsh, created marsh, habitat, hydrologic processes, marsh birds, plant composition

Implications for Practice

- Created marshes provide habitat for many marsh bird species and therefore are an important tool in combating the decline of marsh bird populations due to habitat loss.
- Hydrologic connectivity, water level variability, and specific types of emergent wetland vegetation communities are important components of restoration designs that benefit marsh bird species.

Introduction

Coastal marsh loss occurs at an alarming pace globally, with extremely high rates along the northern Gulf of Mexico, particularly in Louisiana. Louisiana loses 77,000 m^2 of coastal marsh per day, and 28 km^2 per year (Couvillion et al. 2017). Historically, land loss rates were higher, and over 5000 km^2 of coastal marshes have been lost over the last century (Day et al. 2000). Coastal marshes in Louisiana were formed by sediment deposition from the Mississippi River and organic matter accretion (Nyman et al. 2006); however, currently levees have disconnected the river from much of the coastal marsh. The lack of sediment supply, coupled with subsidence, sea level rise, erosion, and tropical storms, has created a coastal landscape that is a mosaic of healthy and degraded marshes (Day et al. 2000; Hiatt et al. 2019). To combat such staggering land loss and coastal degradation, Louisiana initiated a Coastal Master Plan (priced at $50 billion) to protect and restore coastal wetlands (Coastal Protection and Restoration Authority of Louisiana 2023). Louisiana's Coastal Restoration Program has implemented dozens of marsh creation projects (Coastal Protection and Restoration Authority of Louisiana 2023), but efforts seldom consider how construction design influences vegetation and wildlife response. Wildlife consideration, if it occurs, often stems from commercial and recreational hunting and fishing interests. However, recent efforts focused on the development of guidelines for

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creating habitat for non-game species, including marsh birds (Deepwater Horizon Louisiana Trustee Implementation Group 2023). Despite this initiative, the lack of monitoring of wildlife responses to marsh creation design limits the ability of practitioners to improve marsh restoration efforts for taxa such as secretive marsh birds (SMBs).

SMBs are a group of conservation concern because of nationwide population declines and the general lack of knowledge of coastal populations due to the difficulty of studying elusive and secretive species (Conway 2011). On the lower Mobile-Tensaw River Delta in Alabama, populations of SMBs, such as King Rail (*Rallus elegans*), Least Bittern (*Ixobrychus exilis*), and Common Gallinule (*Gallinula galeata*), declined from 2004 to 2015 by 50, 38, and 15%, respectively (Rush et al. 2019). While unexplored, these relationships could be more dramatic in the Mississippi River Delta due to rapid land loss and alterations of existing marshes across this region. Louisiana contains 40% of all wetlands in the conterminous United States (Boesch et al. 1994) and so is important for marsh bird conservation. Consequently, created marshes that satisfy habitat needs of marsh bird species in Louisiana may prevent more dramatic population declines by slowing the trend of coastal wetland loss.

We identified three ecological processes that affect habitat suitability for marsh birds: hydrologic characteristics, plant composition, and habitat structure. While it is well established that hydrologic conditions, such as hydroperiod, can influence the distribution of bird populations (Baschuk et al. 2012), the influence on SMB has received less attention. Hydrologic conditions affect prey availability, foraging ability, and nest success of marsh birds (Rush et al. 2010; Chabot et al. 2014; Patton et al. 2020). Additionally, hydrologic processes influence the composition and structure of vegetation (Edwards & Proffitt 2003; Byerly et al. 2020). Emergent wetland vegetation species can only establish in areas with flooding influence; without water on the landscape, upland species dominate (Van Der Valk 1981). Many marsh birds are specialists and often select for a specific type of emergent vegetation community that provides unique structure vital for nest building, foraging strategies, and cover from predators (Eddleman et al. 1988; Chabot et al. 2014). Habitat structure, such as edge, vegetation density, and presence of woody vegetation, influences whether birds select a certain area. Edge habitats often support submerged and floating aquatic vegetation, which increases density and diversity of nekton communities and provides important foraging opportunities for many marsh bird species (Bolenbaugh et al. 2011; Patton et al. 2020). Additionally, vegetation density affects marsh bird habitat suitability as denser vegetation provides more cover (Pickens & King 2014). The presence of woody vegetation increases the risk of depredation by mammalian and avian predators and does not provide the nesting material and cover that is needed for most marsh birds (Pickens & King 2012). The design and construction of marsh creation sites can have dramatic effects on hydrologic processes, plant composition, and habitat structure and therefore is an important consideration when attempting to create suitable habitat for marsh birds.

Created marshes in Louisiana are often built higher than natural marshes to increase longevity in the face of subsidence and sea level rise (Edwards & Proffitt 2003; Elsey-Quirk et al. 2009). Several studies documented created marsh sites in Louisiana built higher than the tidal range, and as a result, they supported a dryer site unsuitable for emergent wetland vegetation persistence (Elsey-Quirk et al. 2009; Byerly et al. 2020). Additionally, containment dikes line the perimeter of most marsh creation sites, often impeding hydrologic connectivity (Coastal Protection and Restoration Authority of Louisiana 2017). Currently, it is unknown whether these design and construction features promote suitable habitat for marsh bird species.

In this study, we examine whether created marshes in southeastern Louisiana provide suitable habitat for marsh bird species through two main objectives: (1) by comparing hydrologic characteristics, plant composition, and habitat structure between created and reference natural marshes and (2) by determining the effects of hydrologic characteristics, plant composition, and habitat structure on bird relative abundance. We hypothesized that hydrologic characteristics exerted greater influence on the relative abundance of marsh birds than plant composition and habitat structure, as hydrologic factors underlie many aspects of plant composition and habitat structure. Additionally, we hypothesized that created marshes lack the necessary hydrologic conditions to create suitable marsh bird habitat.

Methods

Study Area

Southeastern Louisiana includes marshes east of the Atchafalaya River basin and is comprised of five hydrologic basins that make up the Deltaic Plain of coastal Louisiana: Terrebonne, Barataria, Pontchartrain, Breton Sound, and Mississippi River Delta (Fig. 1). Levees and river control structures restrict the active delta to just the Mississippi River Delta basin, while all other basins in the Deltaic Plain are inactive deltas (Nyman 2014). Due to the freshwater input of the river and the influence of the Gulf of Mexico, marshes in this area span the salinity gradient from fresh to saline, but saltwater intrusion occurs in many areas due to the construction of navigation channels and oil and gas canals (Day et al. 2000). Additionally, high rates of subsidence and relative sea level rise occur in the Deltaic Plain, making it especially vulnerable to degradation (Zou et al. 2015; Jedlikowski et al. 2016).

Southeastern Louisiana is a microtidal system with an average tidal range of 10–20 cm (Wang et al. 1993). Wind and precipitation-driven water fluctuations exert a greater effect on water levels than tides in coastal Louisiana (Hiatt et al. 2019). Strong north winds cause extremely low water levels, draining ponds and exposing mudflats, while southerly winds cause flooding and inundation events where water levels can rise a meter within a few hours (Denes & Caffrey 1988).

We examined 10 created marsh sites and nine reference marsh sites located within the Deltaic Plain of coastal Louisiana (Fig. 1; Table S10). We selected marsh sites to span marsh types across the estuarine gradient (fresh, intermediate, brackish, and saline), to be accessible by small boat, and based on landowner permission. Fresh marsh sites ($n = 4$) occurred within active deltas of the Mississippi River Delta basin, while all intermediate ($n = 9$), brackish ($n = 2$), and saline marsh sites ($n = 4$)

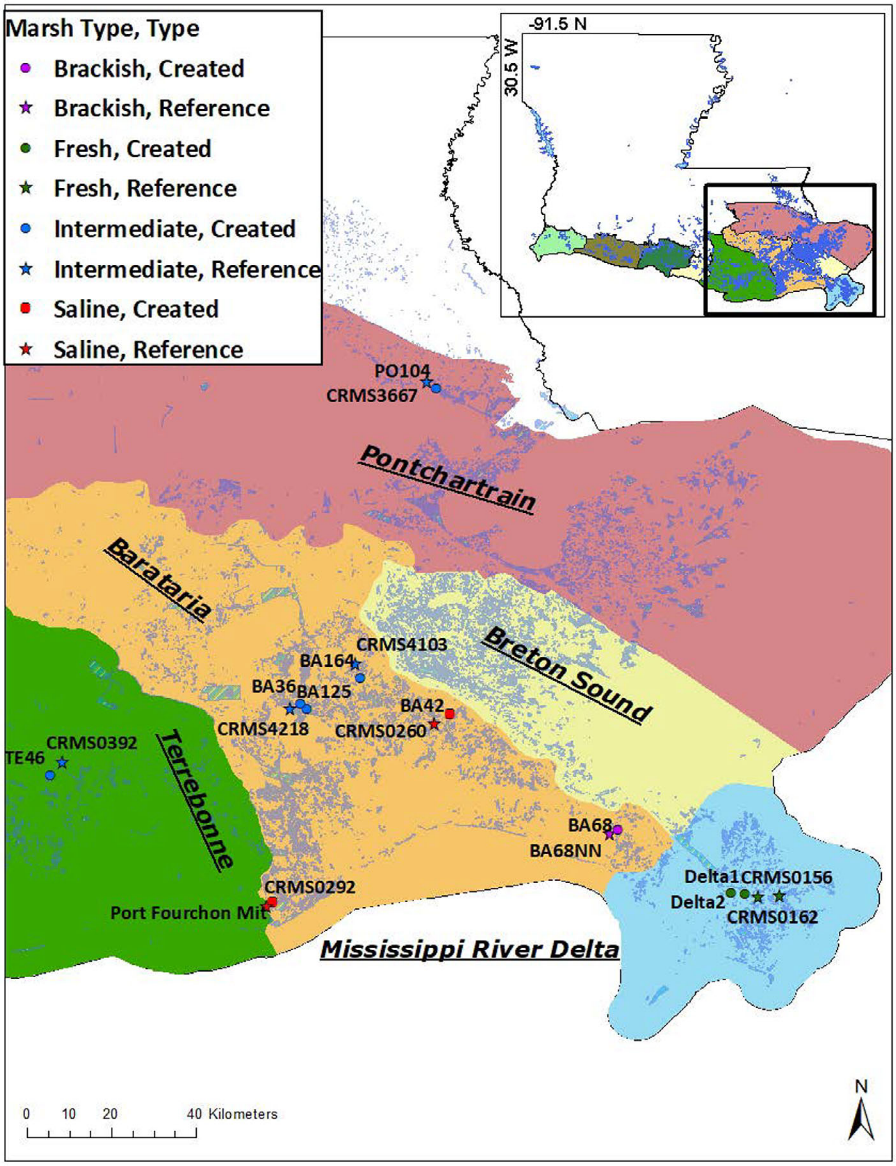

Figure 1. Enlarged view of study area in southeastern Louisiana selected to survey created and reference marshes for marsh bird relative abundance and habitat characteristics during the 2021–2023 breeding seasons (March–June). Map shows the five hydrologic basins that make up the Deltaic Plain of Louisiana: Terrebonne, Barataria, Breton Sound, Pontchartrain, and the Mississippi River Delta. Icons indicate the locations of sites. Shapes and colors represent marsh type and if the site is a created or reference marsh.

occurred within inactive deltas throughout the Terrebonne, Barataria, and Pontchartrain basins (Fig. 1; Table S10). We classified marsh types based on Coastwide Reference Monitoring System (CRMS) marsh classifications, which are determined by vegetation surveys conducted at the CRMS station (U.S. Geological Survey 2006).

Created sites varied in sediment sources and whether containment dikes were used during construction. Both fresh marsh sites constructed from sediment dredged from the navigation channels within the active delta of the Mississippi River and consisted of sandy soils, which negated the need for containment dikes. All non-fresh sites were constructed with sediments dredged from large nearby lakes and consisted largely of fine sediment in addition to some fine sands. These sites all appeared to have been constructed within containment dikes, which often are degraded in strategic locations several years after construction to allow tidal exchange (Coastal Protection and Restoration Authority of Louisiana 2017).

We defined reference sites as marshes that have not been dredged. We chose reference sites located within 1 km of a CRMS station where water levels were recorded hourly (U.S. Geological Survey 2006). One created marsh (BA-68) was over 20 km from the nearest CRMS station of the same marsh type, which precluded pairing it to a CRMS station. Instead, we surveyed the nearest natural marsh, which was approximately 100 m from BA-68 (site name: BA68NN).

Bird Surveys

We conducted bird surveys at all created and reference marsh sites to determine the relative abundance of marsh birds. At each site, we surveyed four randomly generated point locations, which were placed at least 250 m apart to create point independence and minimize double counting of individual birds. For each survey, we recorded visual and auditory detections of all observed birds within the survey plot. We defined survey plots as the area within a 100-m radius of the observer (Conway 2011), which covered a total area of 31,415.93 m^2 (hereafter, "plot"). We surveyed each plot four times during each breeding season (March–June) of 2021–2023. We conducted surveys from 30 minutes before sunrise until 1030 Central Daylight Time (CDT) except during periods of heavy rains or winds greater than 15 kph. We rotated observers and the order that points were surveyed throughout the season to reduce the potential for observer bias and to ensure that sites were surveyed at least once during early morning hours. Observers were trained to identify birds and estimate plot size prior to study initiation.

To increase responses of SMBs, we used the Standardized North American Marsh Bird Monitoring Protocol established by Conway (2011) to perform call-back surveys following a 5-minute passive listening period. We used handheld speakers (Foxpro Inferno, Lewistown, PA, U.S.A.) to broadcast SMB calls, which included in order, Black Rail (*Laterallus jamaicensis*), Least Bittern, King Rail, Clapper Rail (*Rallus crepitans*), Common Gallinule, Purple Gallinule (*Porphyrio martinica*), American Coot (*Fulica americana*), and Pied-billed Grebe (*Podilymbus podiceps*). These calls reflect potential breeding SMB species within this region and can elicit responses from a variety of other SMBs (Conway 2011). We played each call for 30 seconds, followed by 30 seconds of silence and listening (Conway 2011), and continuously recorded all bird species detected throughout the entire survey.

We used the Partners in Flight Avian Conservation Assessment Database (Partners in Flight 2021) to identify which species to include in a marsh specialist guild (hereafter "guild") for analysis (Table 1). We then selected four focal species to make species-specific inferences. These focal species are the breeding SMBs in our study area: Common Gallinule (COGA), Purple Gallinule (PUGA), King/Clapper Rail (KIRA/CLRA), and Least Bittern (LEBI). KIRA and CLRA are nearly impossible to distinguish by call or morphology. KIRA are normally found in fresh marsh and CLRA are normally in salt marsh, but these species have been known to hybridize, especially in intermediate and brackish marshes (Maley 2012). For these reasons, we decided to lump the two species for analysis.

Table 1. List of bird species included in the marsh specialist guild that were detected at our sites in coastal Louisiana during the 2021–2023 breeding seasons (March–June). Birds were classified as marsh specialist based on the Partners in Flight Avian Conservation Assessment Database. Numbers in parentheses are the total number of detections for each species.

	Species included
Marsh specialist (MS) guild	American Bittern (3), Black Tern (1), Black-necked Stilt (18), Boat-tailed Grackle (434), Common Gallinule (1274), Dark Ibis (8), Forster's Tern (8), Fulvous Whistling Duck (2), King/Clapper Rail (945), Least Bittern (268), Marsh Wren (655), Mottled Duck (37), Nelson's Sparrow (13), Pied-billed Grebe (40), Purple Gallinule (126), Seaside Sparrow (345), Sora (164)

Hydrologic Parameters

To determine the effects of hydrologic characteristics on marsh bird relative abundance, we measured instantaneous water depths, hydroperiod, and a modified normalized difference water index (NDWI). To measure instantaneous water levels at the time of the bird surveys, we measured water depth (cm) at the survey point location with a meter stick. To measure hydroperiod throughout the breeding season, we installed water loggers (In-Situ RuggedTROLL 100 pressure transducers) at all created marsh sites that recorded hourly water depth (Lipford 2024). We installed water loggers before March 1 of every year and removed them after the completion of the field season (June 30). In 2021 and 2022, we installed one water logger at each created site. In 2023, we installed two water loggers at each created site and one at each reference site to increase water level data (Lipford 2024). We downloaded hourly water level data from CRMS stations near the reference marshes and, based on their relation to data generated by associated water loggers in 2023, used the data to predict water levels at reference marshes in 2021 and 2022 (Lipford 2024). Gaps in the data exist for several sites where predictions were not possible due to a non-linear relationship between the CRMS station and our site ($n = 3$) and due to the malfunction of several devices ($n = 2$). Data from the water loggers and predictions resulted in 186,117 hourly water depth observations, which we used to calculate daily, weekly, biweekly (every 2 weeks), and monthly mean, median, maximum, minimum, and standard deviation values describing water depths in each plot. To calculate NDWI, we extracted satellite imagery from Harmonized Sentinel-2 MSI (10 m spatial resolution; European Union/ESA/Copernicus) using Google Earth Engine (GEE; Gorelick et al. 2017). We calculated NDWI to measure "wetness," or moisture content, within the entire survey plot area. To establish plot area, we placed 100 m radius buffers around survey points. We filtered dates between February 20th and June 30th for each year (2021, 2022, and 2023) to account for the differing start and end dates within each survey year. We masked cloud cover of over 20% and used mean spectral bands to calculate a modified NDWI ([Band 3 – Band 8]/[Band 3 + Band 8]). We used the modified NDWI because it is able to measure bodies of water more accurately (Xu 2006; Ji et al. 2009). Values ranged from -1 (drought, non-aqueous surfaces) to $+1$ (open, deep water).

Plant Composition

To determine the effects of plant composition on marsh bird relative abundance, we evaluated vegetation communities within each survey plot. In 2022, we collected drone imagery (during the second and fourth survey rounds) of each plot to assist in the classification of vegetation community and to identify the percent woody vegetation. Annually, during the second and fourth survey rounds, we stood at the survey point and drew habitat sketches depicting the composition and configuration of major vegetation types and water inside the plot to ground truth the drone imagery. Based on the drone imagery and habitat sketches, we determined the dominant plant species present within each plot and then classified each plot as one of Snedden's (2019) community types (Table 2). We added a community type (Typha) as four of the points consisted almost entirely of *Typha* sp., which did not fit any of Snedden's (2019) community types (Table 2). For all points ($n = 76$), vegetation communities were: Roseau Cane ($n = 16$), Wiregrass ($n = 14$), Brackish mix ($n = 13$), Three-square ($n = 9$), Oystergrass ($n = 11$), Bulrush ($n = 6$), Typha ($n = 4$), and Bulltongue ($n = 3$). There was some variation in community type, based on classification of points, between created marshes and reference marshes (Table S1).

Habitat Structure

To determine the effects of habitat structure on marsh bird relative abundance, we calculated the median normalized difference vegetation index (NDVI) value during spring, area of edge habitat, and percent vegetated cover for each survey plot. In the same way as NDWI, we extracted these metrics from Harmonized Sentinel-2 MSI satellite imagery using GEE (Gorelick et al. 2017). We calculated median NDVI ([Band 8 – Band 4]/[Band 8 + Band 4]) within plots for each year, which represents an index of "greenness" or density of vegetation. Values ranged from -1 (open water) to $+1$ (dense, green vegetation). We removed open water from each image to restrict our measures to vegetation density within the marsh complex using a threshold metric from the calculated NDVI. We measured the area (square meters) of edge habitat by classifying wetland pixels and water pixels using NDVI and NDWI values, respectively, to create a spectral image analysis with minimum thresholds of -0.2 for wetlands and 0.2 for water. Here, edge is defined as the interface of land and water; area was calculated within a 5 m buffer (2.5 m land and 2.5 m water) of that interface. We then converted area of edge per plot to proportion of edge per plot (0–1) for the analysis. Lastly, from the same NDVI and NDWI values, we calculated the area of cover (vegetated land) from the spectral image analysis and converted them to percent vegetated cover for each plot.

Statistical Analysis

Comparison of Habitat Characteristics Between Created and Reference Marsh. To assess differences in measured variables of hydrologic characteristics, plant composition, and habitat structure between created and reference marshes, we analyzed multiple mixed models comparing habitat variables (NDWI, NDVI, proportion of edge, percent cover, mean monthly water levels, and monthly water level standard deviation) to type (created/reference) as a fixed effect with a random effect of *plot_id* (Table S2). We implemented each model in a Bayesian framework using the brms package (Bürkner 2017) in R (R Core Team 2023). Additionally, we used a Pearson's Chi-squared test of independence to compare vegetation communities between created and reference sites.

Effects of Habitat Characteristics on Marsh Bird Relative Abundance. To determine which water depth covariates demonstrated the greatest effect on bird relative abundance, we used maximum likelihood estimations of Poisson generalized linear models (GLMs) in the lme4 package (Bates et al. 2009). For the guild and each focal species, we tested the effects of mean, median, maximum, minimum, and standard deviation for water depth at three different time periods: weekly, biweekly, and monthly. We then selected the model with the lowest Akaike information criterion (AIC) to be used for the following models (Table S3).

To determine the effects of habitat characteristics on marsh bird relative abundance across created and reference sites, we built generalized linear mixed models (GLMMs) in a Bayesian framework using the brms package (Bürkner 2017) in R

Table 2. Dominant plant species included in each vegetation community type as defined by Snedden (2019). Asterisk represents the community type that we added. Community types are arranged by increasing salinity. Vegetation community is the name of the classification; dominant species are the seven most abundant taxa for each community type as defined by Snedden (2019). Bolded values represent species that comprised greater than 70% of the community.

Vegetation community	*Dominant species*
Bulltongue	***Sagittaria lancifolia***, ***Persicaria punctatum***, ***Alternanthera philoxeroides***, ***Ludwigia grandiflora***, **Typha sp.**, ***Colocasia esculenta***, ***Sacciolepis striata***
Three-square	***Schoenoplectus americanus***, ***Spartina patens***, ***S. lancifolia***, ***Lythrum lineare***, ***Cladium mariscus***, ***Eleocharis macrostachya***, ***Distichlis spicata***
Roseau Cane	***Phragmites australis***, *S. patens*, *A. philoxeroides*, *Spartina alterniflora*, *Typha domingensis*, *Zizaniopsis miliacea*, *P. punctatum*
Typha*	**Typha sp.**, ***P. australis***, *Iva frutescens*, *Ipomoea sagittata*, *S. patens*, *S. americanus*, *Rumex* sp.
Wiregrass	***S. patens***, ***D. spicata***, *S. americanus*, *Bolboschoenus robustus*, *I. sagittata*, *L. lineare*, *S. alterniflora*
Bulrush	***B. robustus***, ***D. spicata***, ***S. patens***, *S. cynosuroides*, *S. alterniflora*, *Paspalum distichum*, *Juncus roemerianus*
Brackish Mix	***S. alterniflora***, ***S. patens***, *J. roemerianus*, *D. spicata*, *B. robustus*, *Avicennia germinans*, *I. frutescens*
Oystergrass	***S. alterniflora***, *J. roemerianus*, *S. patens*, *D. spicata*, *Batis maritima*, *B. robustus*, *A. germinans*

(R Core Team 2023). We opted to use relative abundance, which accounts for imperfect detection, since we do not need to know the true abundance to determine an unbiased estimate of the relationship between habitat variables and relative abundance (Barker et al. 2018). For the guild and each focal species, we developed a set of candidate models based on four a priori hypotheses on the drivers of bird relative abundance among our sites. Before fitting candidate model sets, we used Pearson's and point biserial correlation coefficients (Welkowitz et al. 2011; Dormann et al. 2013) to assess collinearity of covariates, ensuring that $|r|$ less than 0.7 (Table S4). Because marsh type was correlated with vegetation community, we used maximum likelihood estimates of GLMs to determine which variable was a better predictor of bird relative abundance. We found that vegetation community was a better predictor of bird relative abundance (ΔAIC $= -38$); therefore, we elected to use this variable in all subsequent models (Table S5). Additionally, we evaluated the most appropriate distribution for each guild and focal species by comparing the AIC of intercept-only maximum likelihood estimations for Poisson, negative binomial, zero-inflated Poisson, and zero-inflated negative binomial and selected the distribution with the lowest AIC (Fowler et al. 2024; Table S6).

We chose random effects structure by comparing interclass correlation coefficient (ICC) values, which we used as a diagnostic to quantify the amount of variation explained by a specific random effect (Midway 2022). We only included random effects that substantially decreased the model error term (ICC values >0.5). We evaluated random effect structures including *plot_id*, *survey round*, *observer*, and *pair*, but these variables demonstrated nominal effects as indicated by their ICC values (Table S7). Therefore, to facilitate model parsimony and convergence, we elected to only use *plot_id* in all subsequent models. *Plot_id* represented a unique ID for site, survey point, and year to account for variation among sites and year.

Our first model hypothesized that bird relative abundance was solely influenced by hydrologic characteristics. Fixed effects included in this model were *type* (2-level categorical; created and reference), *water depth at survey*, *median spring NDWI* (NDVI within plot), and the selected water depth variable for each guild or species. Our second model hypothesized that bird relative abundance was solely influenced by plant composition. Fixed effects included in this model were *type*, and *vegetation community*. Our third model hypothesized that bird relative abundance was solely influenced by habitat structure, and fixed effects included in this model were *type*, *proportion of edge* (proportion per plot), *percent cover* (percent per survey plot), *median spring NDVI* (NDVI within plot), and greater than *25% woody vegetation* (2-level categorical: true if plot was >25%, false otherwise). Our final model hypothesized that a combination of hydrologic characteristics, plant composition, and habitat structure collectively influence bird relative abundance, and for this model we chose one parameter from each of the previous models. We used maximum likelihood beta coefficient estimates of GLMs to determine which variable was the best predictor of each guild/focal species relative abundance, and therefore the combination model differed between species. The four modeled hypotheses were compared to an informed null model, which only contained *type* as a fixed effect. We included *type* in all models to evaluate whether there was a difference in bird relative abundance between created and reference marshes and to compare the relative effect size of *type* compared to other habitat variables.

For each candidate model, we ran four Markov Chain Monte Carlo (MCMC) chains of 3000 iterations and used uninformative priors. We examined model convergence using trace plots, the Gelman-Rubin statistic ($\widehat{R}$ value <1.1; Gelman & Rubin 1992), and the number of effective samples. For each focal species and guild, we ranked models using approximate Leave-One-Out (LOO) cross-validation in the loo package (Vehtari et al. 2017). We used the expected log pointwise predictive density (ELPD) to rank models and selected the model with the lowest ELPD. Models within four ELPD of the top model were considered to be competitive (Vehtari et al. 2017), and for the marsh specialist guild and some of the focal species, there were two top competing models (Table S8). In these cases, we built a new model using all parameters from each competitive model and examined the posterior distributions of each covariate estimate for this final model. Posterior estimates with 95% credible intervals (CRIs) that did not overlap 0 were considered to significantly influence relative abundance. Additionally, we built GLMMs; with just *vegetation community* to understand the absolute value effect of different vegetation communities on bird relative abundance. Oystergrass had to be excluded from the COGA models because of low detections and convergence issues.

Results

We completed 766 surveys (created = 413, reference = 353), including 166 in 2021, 299 in 2022, and 301 in 2023. Across all years, we detected 4341 individuals of 17 species which comprised the marsh specialist guild (Table 1). Our most abundant focal species was COGA ($n = 1274$), followed by KIRA/CLRA ($n = 945$), LEBI ($n = 268$), and PUGA ($n = 126$). Average detections did not vary greatly between created and reference sites for the guild or any focal species (Fig. S1). Overall, created and reference sites in the active delta of the Mississippi River supported the highest relative abundances of marsh birds.

Comparison of Habitat Characteristics Between Created and Reference Marsh

Water levels varied among years and among sites (Fig. 2). Mean water levels were not statistically different between created (6.9 cm) and reference (7.6 cm) sites but standard deviation was lower at created sites (1.5 cm) than at reference sites (2.5 cm; Table S2; Fig. S2). The maximum water depth of 73.5 cm was recorded (24 April 2023) at a created site in the Mississippi River Delta basin (Delta-1D).

Created sites had higher NDVI, edge, and cover than reference sites (Fig. S3). Median spring NDWI was higher at reference sites ($\bar{x} = -0.22$, range $= -0.57$ to 0.19) than created sites ($\bar{x} = -0.39$, range $= -0.72$ to 0.19; Table S2; Fig. S2).

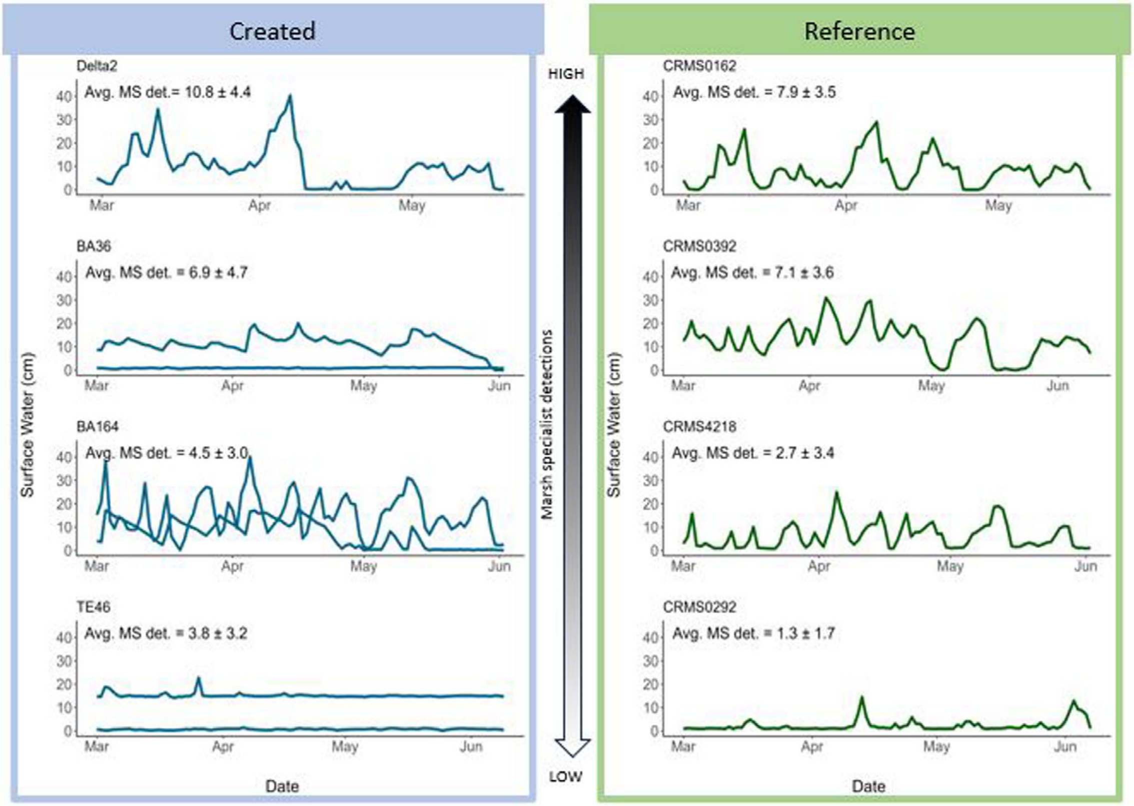

Figure 2. Hydroperiods from four created and four reference marsh sites in coastal Louisiana with their corresponding marsh specialist detections. Lines represent surface water levels throughout the 2023 breeding season, and graphs with two lines represent sites with two water loggers. Avg. MS det. = average marsh specialist detections for each site.

Median spring NDVI was higher at created sites ($\bar{x} = 0.53$, range = 0.24–0.81) than reference sites ($\bar{x} = 0.41$, range = 0.09–0.70; Table S2; Figs. 4 & 5). Reference sites had more edge ($\bar{x} = 0.14$, range = 0.0–0.26) than created sites ($\bar{x} = 0.08$, range = 0.008–0.2; Table S2; Fig. S2). Likewise, created sites had more cover ($\bar{x} = 68\%$, range = 36–88%) than reference sites ($\bar{x} = 55\%$, range = 28–77%; Table S2; Fig. S2).

Vegetation communities were also variable among created and reference sites ($\chi^2 = 18.931$, degrees of freedom [*df*] = 8, $p = 0.015$). Only one site (created: BA-164) was classified as Typha, and only one site (reference: CRMS4103) was classified as Bulltongue. Bulrush, Brackish Mix, Three-square, Wiregrass, Oystergrass, and Roseau Cane were found at created and reference sites.

Effects of Habitat Characteristics on Marsh Bird Relative Abundance

The combination model and the hydrologic characteristics model were the top two competing models for predicting the relative abundance of the marsh specialist guild (Table S8). After these models were combined, vegetation community (Table S9; Fig. 3) and standard deviation of monthly water depth (Table S9; Fig. 4) had a positive effect on marsh specialist relative abundance. Marsh specialist species were most abundant in Roseau Cane and Wiregrass communities, but all vegetation communities had a positive effect on the relative abundance of this guild (Figs. 3 & 5).

The top model for COGA was the combination model, indicating that hydrologic characteristics, plant composition, and habitat structure collectively influence COGA relative abundance (Table S8). Monthly water depth standard deviation (SD; Table S9; Fig. 4) and some vegetation communities (Table S9; Fig. 3) had a positive effect on COGA relative abundance. COGA were most abundant in Roseau Cane and Wiregrass communities, while Brackish Mix, Bulrush, and Three-square communities had a negative effect on COGA relative abundance (Figs. 3 & 5).

The top model for KIRA/CLRA was the combination model, indicating that hydrologic characteristics, plant composition, and habitat structure collectively influence KIRA/CLRA relative abundance (Table S8). Vegetation community was the only variable that affected KIRA/CLRA relative abundance (Table S9; Fig. 3). KIRA/CLRA were most abundant in Brackish Mix and Oystergrass communities, while Wiregrass and Roseau Cane communities had a negative effect on rail relative abundance (Figs. 3 & 5).

The combination model and the hydrologic characteristics model were the top two competing models for LEBI (Table S8). After these models were combined, monthly maximum water depth had a positive effect on LEBI relative

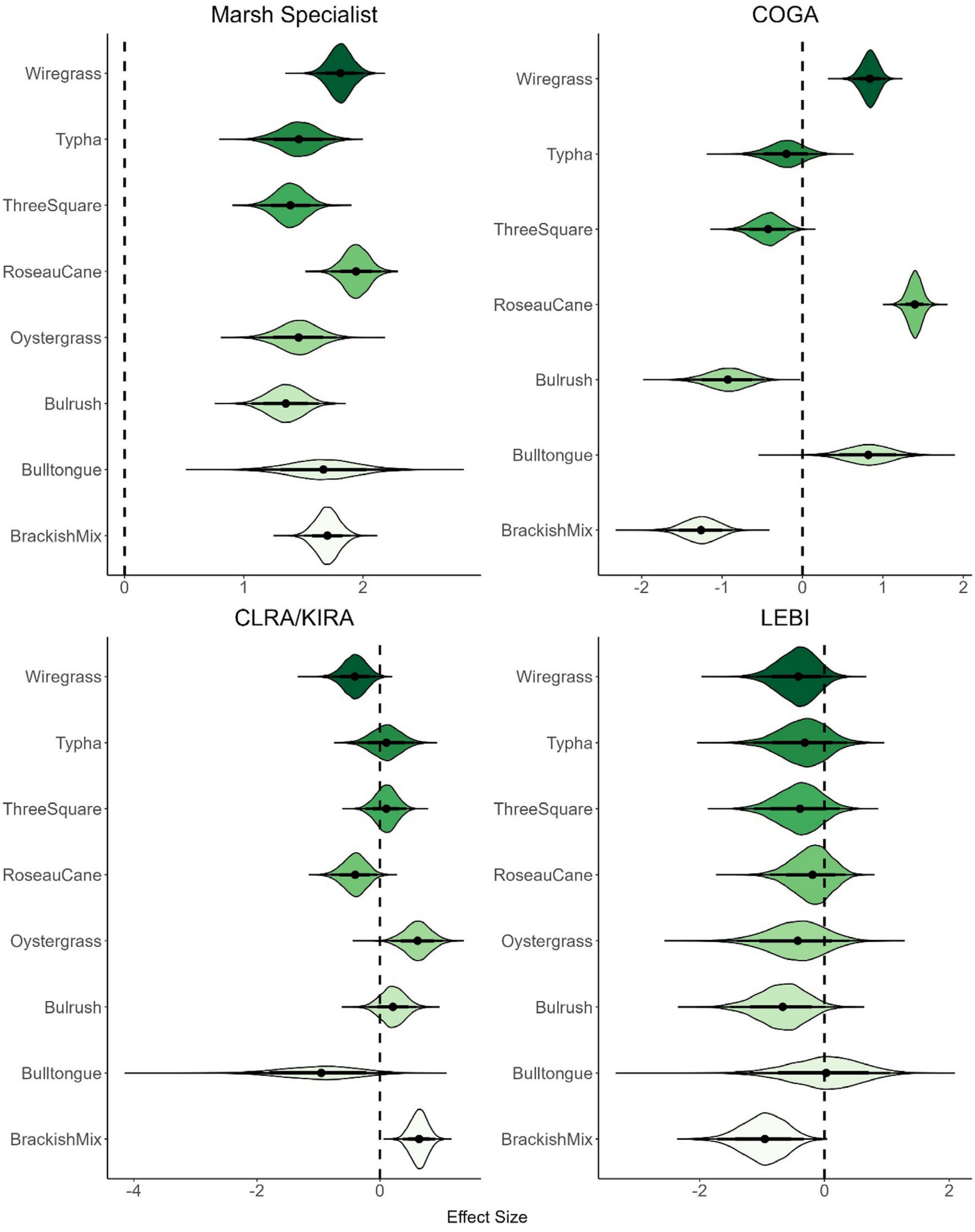

Figure 3. Effect of vegetation community on relative abundance of marsh specialists, Common Gallinule (COGA), Clapper/King Rail (KIRA/CLRA), and Least Bittern (LEBI) at created and reference marsh sites in coastal Louisiana during the 2021–2023 breeding seasons (March–June). Each eye plot represents the posterior distribution for each vegetation community, with the center dot indicating the beta coefficient and the tails indicating the upper and lower 95% credible intervals (CRIs). Estimates are from models run with just *vegetation community*. The dotted line represents 0 and 95% CRIs that overlap 0 are not significant. Vegetation community distributions that are above 0 positively affect relative abundance, while distributions below 0 negatively affect guild.

abundance (Table S9; Fig. 3). There were no positive associations between vegetation communities and LEBI relative abundance, but Brackish Mix had a negative effect on the relative abundance of this species (Fig. 3).

All other habitat variables did not have a significant effect on marsh bird relative abundance, including whether a site was created or not (Table S9). Bird relative abundance did not differ between created and reference sites for the guild or any focal

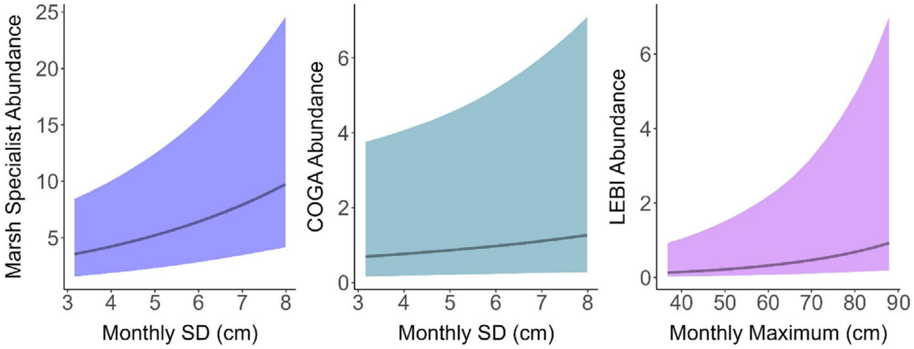

Figure 4. Effect of monthly water depth variables on marsh specialists, Common Gallinule (COGA) and Least Bittern (LEBI) relative abundance at created and reference marsh sites in coastal Louisiana during the 2021–2023 breeding seasons (March–June). Regression lines show the mean posterior estimates of each parameter from the model, and shaded areas depict the 95% credible intervals (CRIs) of the posteriors.

species. Additionally, there were too few detections of Purple Gallinules ($n = 126$) to include in any formal analysis.

Discussion

The results of our study indicate that hydrologic variation and vegetation communities are the drivers of marsh bird relative abundance regardless of whether a marsh is created or not. While vegetation communities, monthly water level SD, NDWI, NDVI, edge, and cover differed between created and reference sites, our results indicated that created marshes can support similar relative abundances of marsh birds as reference sites, depending on what habitat features are present at the site.

Long-term hydrologic characteristics were important drivers of marsh bird relative abundance, with more variation resulting in higher marsh bird relative abundances. Water depths play a crucial role in marsh bird relative abundance (Timmermans et al. 2008; Baschuk et al. 2012); however, few studies have investigated bird responses to hydroperiod and instead focus on static water depths. Pickens and King (2014) found that long-term

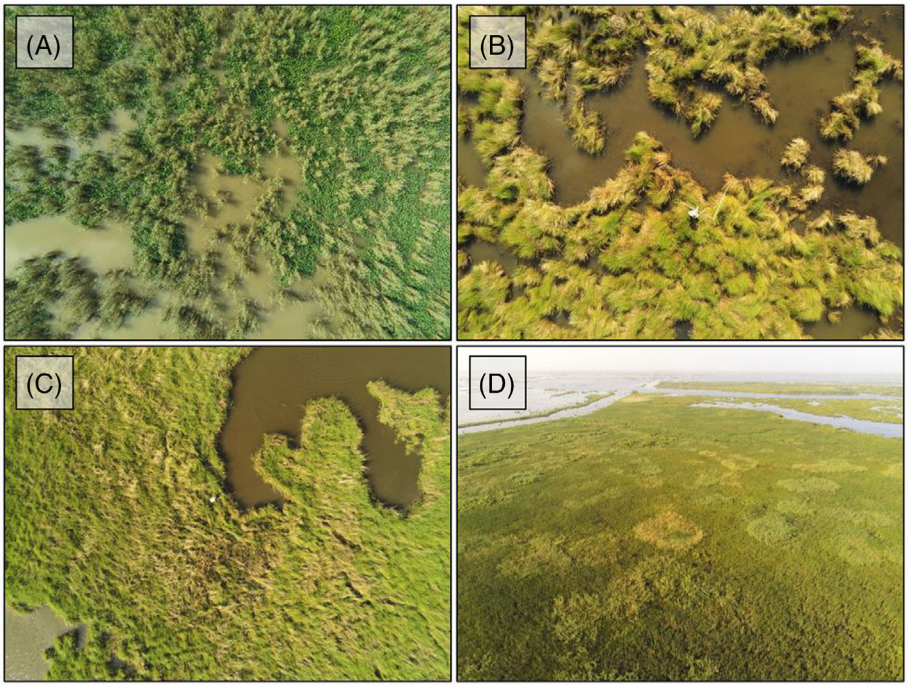

Figure 5. Aerial photographs of plots surveyed for marsh bird relative abundance in coastal Louisiana during the 2021–2023 breeding seasons (March–June). Photographs represent four different types of vegetation communities: (A) plot classified as Roseau Cane; lighter green is *Phragmites* sp. and darker green is floating aquatic vegetation; (B) plot classified as Wiregrass; vegetation clumps are *Spartina patens*; (C) plot classified as Oystergrass; vegetation is mostly *S. alterniflora*, darker area is *Juncus roemerianus*; (D) site classified as Typha; vegetation is mostly *Typha* sp. with lighter green circular patches of *Phragmites* sp. Photographed by A.L.

hydrologic metrics were better predictors of bird relative abundance than instantaneous water depths, and this was also the case with our study. Similarly, our results show that many marsh bird species selected sites that have more dynamic hydrologic regimes, as water depth (monthly SD) was positively associated with the relative abundance of the marsh specialist guild and COGA. Monthly SD is a measure of variability in water depths, as sites with higher monthly SD will have greater fluctuations in water levels and more dramatic flooding and drying events. While varying water depths are important, the mean that these depths fluctuate around also affects marsh bird presence, because deeper water excludes certain species (Norazlimi & Ramli 2015). For example, KIRA/CLRA preferred sites with lower NDWI, meaning areas with shallow water or no water. Conversely, LEBI relative abundance increased with increasing monthly maximum water depth, which is not surprising as this species is associated with minimum depths of 20–30 cm (Chabot et al. 2014; Pickens & King 2014). LEBI were abundant at plots with maximum water depths of 40 cm and had high relative abundances in plots with maximum depths of 50–90 cm. While hydrologic variability is beneficial, extreme flooding can also be detrimental, killing emergent vegetation and causing bird nest failure (Gathman et al. 2005; Rush et al. 2010). Sites that provide variable water levels around a shallow water level mean or areas with both deep and shallow water will promote an abundance of marsh specialist species and SMB.

Plant composition was another important factor driving marsh bird relative abundance. Plant communities can be affected by hydroperiod and salinity (Baldwin et al. 1996), and marsh birds may be selecting for sites that are characterized by fluctuating water levels because of the vegetation community that these flooding regimes support. Variability in water levels will favor some types of wetland vegetation communities over others, as plant species are adapted to different frequencies and depths of flooding (Gathman et al. 2005). Stable flooded conditions lead either to open water or often to monocultures of cattail (*Typha* sp.), cutgrass (*Zizaniopsis miliacea*), or other robust emergent vegetation (Li et al. 2004), whereas stable non-flooded conditions promote woody encroachment and support few wetland-dependent species (Elsey-Quirk et al. 2009). While we did not find that woody vegetation played a significant role in marsh bird habitat selection, studies in other ecological systems found that marsh birds are negatively associated with increasing woody vegetation presumably due to the potential increase in mammalian and aerial predators (Pickens & King 2012). Some of our sites that had KIRA/CLRA present supported woody vegetation at the upper end of the elevation gradient but were often juxtaposed to sloping banks that supported shallow emergent marsh. However, restoration sites with dynamic flooding regimes can decrease woody encroachment and promote vegetation communities that are crucial to marsh bird habitat (Malone et al. 2021).

Roseau Cane, which is the common name for Louisiana's native *Phragmites* sp., hosted the highest relative abundances of marsh specialist species. In North America, a European lineage of *Phragmites* often creates a dense monoculture habitat that negatively impacts marsh bird abundance (Benoit & Askins 1999; Robichaud & Rooney 2017). However, in Louisiana, Roseau Cane generally is either the Delta lineage or the Gulf/Land lineage (Knight et al. 2018). The Roseau Cane communities that we studied were often characterized as having deep and shallow water areas that support submerged and floating aquatic vegetation, an important aspect of marsh bird foraging and nesting behavior.

Our study also found Wiregrass communities to be important for marsh specialists and COGA habitat. Many of these sites were characterized by thick clumps of *Spartina patens* often surrounded by flooded and ponded areas, which provide areas of cover and areas of open water foraging that benefit marsh bird species such as COGA. However, KIRA/CLRA were negatively associated with Wiregrass communities, which supports Pickens and King (2013) finding. KIRA/CLRA were most abundant in Oystergrass and Brackish Mix communities, both of which are found in higher salinities. However, this may be a bias of lumping the two species, as we detected many more CLRA/KIRA in more saline marshes, and CLRA are considered salt marsh specialists (Meanley & Wetherbee 1962).

Numerous studies have documented the use of *Typha* sp. by marsh birds, including LEBI and COGA (Valente et al. 2011; Chabot et al. 2014; Malone et al. 2021); however, our results showed a negative association for both of these species. *Typha* sp. thrives in areas where there is constant deeper flooding, and in some systems creates a dense monoculture where it outcompetes other emergent plants (Li et al. 2004), which is more characteristic of our study plots classified as Typha. The high density of vegetation and lack of open water areas may explain why marsh birds were not favoring Typha plots. Our results also indicated LEBI and COGA were negatively associated with Bulrush habitats. Two of the Bulrush plots never flooded during our study, explaining the absence of birds that require flooded habitats and emphasizing the importance of not generalizing about the value of vegetation communities without consideration of hydrologic processes. Surprisingly, LEBI had no positive associations with any vegetation community, but several recent studies indicate that LEBI may be more of a habitat generalist than previously thought. However, LEBIs still require some emergent vegetation structure to be present (Valente et al. 2011; Rush et al. 2019).

When compared to the effects of hydrologic characteristics and vegetation community, our results showed that habitat structure (i.e. NDVI, edge, cover, and woody vegetation) did not significantly influence marsh bird relative abundance across Louisiana's estuarine gradient. This is contradictory to other studies that have found edge habitat, cover, NDVI, and woody vegetation to be important factors in marsh bird habitat (Pickens & King 2012; Leveau et al. 2018; Patton et al. 2020). It may be that habitat structure measured at the plot level (31,415.93 m^2) was not representative of habitat structure within bird home ranges. Our study design precluded multi-scale habitat evaluations because our points were spaced as close as 250 m apart; however, future studies may benefit from assessing edge habitat at multiple spatial scales (Pickens & King 2012, 2014; Jedlikowski et al. 2016). Additionally, if the relationship between these habitat variables and bird relative abundance is not linear, effects could have been masked by our linear models. For example, marsh birds need some amount of edge habitat, but large amounts of edge can be an indicator of a degrading or subsiding marsh that has little marsh bird habitat, especially in more saline environments (Benoit & Askins 2002; Sapkota & White 2019). Similarly, marsh birds require enough cover for nesting and protection from predators, but extremely dense vegetation leads to lower abundances of some marsh bird species (Pickens & King 2014), potentially because they are unable to move throughout and forage on the ground. The small range in proportion of edge habitat among our sites may also have contributed to our failure to detect an edge effect. The age of marsh creation sites has also been shown to affect vegetation structure as vegetation changes with succession (Van der Valk 1998). Age could have played a role at our sites; however, we did not have sufficient data to examine this effect in our analysis. Even though our results did not find habitat structure to be a driving factor of marsh bird relative abundance, we believe that it plays an important role, most likely on a broader scale.

Our study occurred during a period of climate variability, which likely played a role in changes in habitat characteristics and marsh bird populations. Hurricane Ida made landfall in our study area as a category 4 storm in August 2021. However, it is difficult to assess the impacts of the hurricane as it occurred between one of the wettest (2021) and dryest (2022) years recorded in Louisiana. Due to the length of our study, we do not have sufficient data to assess how these climatic factors could have played a role in our results. Longer-term studies would be beneficial in understanding the impacts of climate variability on the relative abundance of marsh birds.

Whether a site was created or not was not a predictor of marsh bird relative abundance, meaning that created marshes supported similar relative abundances of marsh birds as reference sites. Other studies found that created marshes support less bird diversity and abundance than natural marshes (Desrochers et al. 2008; Sebastián-González & Green 2016; Giosa et al. 2018), but this was not the overall case for our study. However, many of our reference sites are degraded and subsiding, and thus provide lower-quality habitat. Additionally, it is hard to generalize across all created or reference sites as we identified substantial variation among habitat variables among sites. While some created marshes supported high relative abundances of marsh birds, other sites lacked the habitat conditions that promote suitable habitat for marsh birds. Our study emphasizes that quantifying specific abiotic processes (e.g. hydrologic processes), plant composition, and habitat structure provides more informative comparisons of drivers of avian relative abundance than simply if a site is restored or not.

While we did not statistically test for effect across hydrologic basins, we found that our top four sites for marsh bird detections occurred in the active delta of the Mississippi River, which could be due to their hydrologic connectivity to the Mississippi River and high concentrations of Roseau Cane communities. Sites in the delta supported dynamic hydrologic regimes and some of the highest water depth monthly SDs. Additionally, all these sites consisted of Roseau Cane communities interspersed with shallow, vegetated, and open water areas, which collectively provide for foraging, nesting, and cover needs for a variety of marsh bird species. These patches of open water have resulted from an invasive scale (*Nipponaclerda biwakoensis*) that caused a recent dieback of Roseau Cane in the MRD (Knight et al. 2018) and are used by marsh birds. Nonetheless, marsh birds use *Phragmites* extensively in other areas along the Gulf Coast where die-back has not occurred (Rush et al. 2019), and healthy Roseau Cane communities could be important habitat in the Mississippi River Delta as well.

Both created marsh sites on Delta National Wildlife Refuge (NWR) in the active delta of the Mississippi River were designed and constructed to benefit wildlife habitat and both supported higher detections of marsh birds than any other sites (including reference) that we studied. These sites were built with a finger design, where strips of land are built with water in between, increasing both edge habitat and shallow water areas. Both sites appeared to be extremely productive marsh systems, and these design features could promote marsh bird habitat in future restoration projects.

Our study demonstrates the importance of creating marshes that promote hydrologic connectivity and water level variability across the estuarine gradient, which in turn supports a variety of emergent vegetation communities and provides suitable habitat for a variety of marsh bird species. Engineered marshes often supported the highest numbers of marsh birds in our study, but several sites supported few birds, which could be due to a variety of factors, including marsh design and construction. Other studies have found that building marsh elevation levels within the tidal range and removing/limiting containment dikes increased hydrologic connectivity and emergent vegetation establishment at created sites (Campbell et al. 2005; Byerly et al. 2020). Additionally, several studies noted that inclusion of tidal creeks and ponds on restored sites help create habitat heterogeneity and hydrologic connectivity (Minello et al. 1994; Boyer & Zedler 1999; Byerly et al. 2020). These features, along with the finger design used at sites in Delta NWR, may promote the creation of more consistent habitat for marsh birds.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Survey plots included in each vegetation community.
Table S2. Posterior estimate, standard deviation (SD), and 95% credible intervals (CRIs) of type (created/reference) for each habitat characteristic.
Table S3. Akaike information criterion (AIC) values for generalized linear models (GLMs) testing water depth variables from water loggers for focal species and marsh specialist guild.
Table S4. Correlation matrix for all habitat variables used in candidate models.
Table S5. Akaike information criterion (AIC) values for generalized linear models (GLMs) testing whether marsh type or vegetation community was a better predictor of abundance.
Table S6. Akaike information criterion (AIC) values for different distributions for each guild and focal species in coastal Louisiana marshes.
Table S7. Interclass correlation coefficient (ICC) values for *observer*, *survey round*, *plot_id*, and *pair* for the guild and focal species in coastal Louisiana marshes.
Table S8. Model selection results for the marsh specialist guild and the focal species abundance.
Table S9. Posterior estimate, standard deviation (SD), and 95% credible intervals (CRIs) of model parameters for each focal species and guild.

Table S10. Marsh type, hydrologic basin, and age (date construction was completed) for all created sites in coastal Louisiana.

Figure S1. Mean detections at created and reference marsh sites for focal species and marsh specialist guild surveyed in coastal Louisiana during the 2021–2023 breeding seasons (March–June).

Figure S2. Comparison of habitat characteristics between created and reference marsh sites in coastal Louisiana across all years (2021–2023).

Figure S3. Aerial photograph of a reference site (left of main channel; BA68NN) and a created site (right of main channel; BA-68) located within the Barataria Basin in coastal Louisiana.

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