APPLIED WETLAND SCIENCE



Living on the Edge: Multi-Scale Analyses of Bird Habitat Use in Coastal Marshes of Barataria Basin, Louisiana, USA

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Received: 14 February 2020 / Accepted: 2 June 2020 / Published online: 27 June 2020 \odot US Government 2020

Abstract

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Coastal marsh loss, combined with expected sea-level rise, will cause inundation and extensive shifts to vegetation and salinity regimes that may affect bird species dependent on coastal ecosystems worldwide. Within coastal-marsh habitats, birds provide key targets for coastal management goals. However, limited information on bird-habitat relationships within coastal marshes inhibits the development of restoration projects targeted to bird species. We surveyed birds bi-monthly within Barataria Basin, LA from July 2014 to December 2015 to compare their use between fresh and saline coastal marshes. Additionally, we examined habitat use at finer spatial scales to assess preference for marsh-edge microhabitats. Edge habitat supported 1.8 times more bird species (guild) richness than emergent and open-water habitat. We concluded that future modelling efforts would be improved if models incorporate edge effects for birds in coastal marshes that extend 20 m from emergent vegetation into open water, with a reduced effect if marsh types convert from fresh to saline. Our data will be useful to simulate the effects of changes in marsh type, area, and edge on habitat quality for birds in coastal Louisiana and will inform habitat restoration and management decisions aimed at optimizing bird use.

Keywords Aquatic vegetation · Barataria Basin · Birds · Coastal marshes · Edge effect · Emergent vegetation

Introduction

Within the United States, coastal habitats support bird communities by providing vital breeding, nesting, foraging, and loafing habitat for 75% of North American waterfowl (i.e., ducks and geese) and other migratory birds (Stedman and Dahl 2013). Wetlands (i.e., marshes and swamps) have been

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s13157-020-01324-2) contains supplementary material, which is available to authorized users.

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lost across most states with 71% of those losses from 1998 to 2004 occurring in coastal wetlands of the Gulf of Mexico (Stedman and Dahl 2013). Louisiana has experienced the greatest loss in wetlands at a rate of 28.06 km² yr⁻¹, and the trend is expected to continue (Couvillion et al. 2017). Additionally, most coastal states are also experiencing shifts in marsh types with much of this shift being from saline to fresh (e.g., Warren et al. 2002). Such changes do occur in Louisiana (Visser et al. 1999), but, in contrast, changes from fresh to saline marsh types dominate (Visser et al. 1998, Visser et al. 2000). Louisiana historically contained the majority of coastal saline and fresh marshes in the conterminous United States with an estimated 39% and 44%, respectively (Field et al. 1988). Marsh loss, combined with large shifts in vegetation and salinity regimes (Couvillion et al. 2013, Visser et al. 2013) will likely affect wildlife species in coastal Louisiana (Nyman et al. 2013), as well as other coastal states.

Over 400 species of birds make use of Louisiana habitats during some part of the year and coastal Louisiana supports up to two thirds of the regional and global abundance of species that use coastal habitats (Gosselink et al. 1998, Remsen et al. 2019). Waterfowl have been the focus of much of the research in Louisiana (Palmisano 1973, Lowery 1974, Esters 1986, Chabreck et al. 1989) because, historically, Louisiana provided a plethora of habitat for waterfowl. With continued habitat loss, bird populations within Louisiana may decline due to increased competition for waning resources (Chabreck et al. 1989). Additionally, there are 34 bird species of conservation concern that use marsh habitat within Louisiana, including wading birds, shorebirds, and passerines (USFWS 2008, Rosenberg et al. 2014), that could be affected by the loss of Louisiana's coastal land.

Currently, the state of Louisiana remains engaged in a significant restoration program that is outlined in the Coastal Master Plan last revised in 2017 (CPRA 2017). This restoration program focuses primarily on socioeconomic impacts in Louisiana and only considers the habitat needs for a few key bird species: mottled duck (Anas fulvigula), green-winged teal (Anas crecca), roseate spoonbill (Platalea ajaja), gadwall (Anas strepera), brown pelican (Pelecanus occidentalis), and the collectively grouped neotropical migrant songbirds (CPRA 2012, 2017). The habitat-suitability indices used to model these birds generally accounted for differences in suitability among marsh types (CPRA 2012). However, in coastal marshes, the edge (interface between emergent vegetation and open water) has been shown to support greater densities of waterbirds (O'Connell and Nyman 2010, 2011) and their prey (Baltz et al.1993). Nonetheless, except for the roseate spoonbill, the positive association of birds with edge habitat was ignored in most habitat restoration models (CPRA 2012, 2017).

Birds are often used as a metric for assessing habitat health and restoration success (Pierce and Gawlik 2010) and comparing the desirability of different restoration options (Nyman et al. 2013). To accurately use birds as indicator species, however, requires regionally specific habitat relationships. Few studies have compared open water to edge habitats (Weller and Spatcher 1965, O'Connell and Nyman 2010, 2011, and Sullivan 2015). Further, we are unaware of any studies that compare bird use of edge habitats with interior emergent vegetation habitats in coastal marshes, which precludes using edge data to estimate the effects of marsh loss on birds. This is a key knowledge gap in bird conservation and management because it is not currently possible to predict effects of habitat conversion from emergent marsh to open water on birds, or to predict the response of birds to management or restoration that alters salinity and the extent of edge habitats. Coastal marshes across Louisiana support extensive bird species; understanding microhabitat and environmental drivers of bird assemblages would provide an important tool for managing coastal marshes.

Most bird species tend to select habitat progressively from coarser to finer spatial scales (Johnson 1980, Battin 2006). Understanding the mechanisms by which marsh ecosystem drivers such as salinity, water depth, and vegetation richness and structure affect bird use is essential for understanding why these birds select some habitats and avoid others. While some fine scale habitat factors that influence birds, such as water level, have been well studied, the importance of other factors such as vegetative structure, is only known for specific groups of birds, based on short-term studies during peak use (Bancroft et al. 2002, Bolduc and Afton 2004, Lantz et al. 2010, Rajpar and Zakaria 2011, Zakaria and Rajpar 2013). Focusing study efforts on fine spatial scales while combining factors across several scales and seasons can provide further insight into habitat use across changing landscapes throughout the year and improve modelling efficacy (Pickens and King 2014).

The aim of this study was to describe bird use within marshes of Barataria Basin, Louisiana. We compared birdhabitat use of fresh and saline coastal marshes. Additionally, we examined habitat use at finer spatial scales to assess preference for marsh-edge microhabitats when compared to openwater microhabitats and emergent-vegetation microhabitats. Our objectives were to 1) determine what marsh-habitat predictors best explain variation in bird density and species richness within Louisiana coastal marshes; and 2) within salinity and microhabitats, determine what fine-scale environmental factors explain variability in bird-assemblage composition. We hypothesized that 1) edge microhabitats would support greater density and richness of birds; and 2) that water depth, submerged aquatic vegetation (SAV), and salinity would be significant variables in explaining bird species and guild composition within Louisiana coastal marshes.

Methods

Study Area

Our study was conducted in the Barataria Basin located in southeastern Louisiana, which is flanked on the east by the active-but-leveed Mississippi River and on the west by the abandoned Bayou Lafourche distributary (Conner and Day 1987) (Fig. 1). Barataria Basin is comprised of 6333 km² coastal marshes and adjacent open-water habitats that span the entire range of salinity regimes. Roughly 701 km² is comprised of fresh-marsh habitat and 541 km² is comprised of saline-marsh habitat (Sasser et al. 2014).

Site Selection

Study sites were selected by identifying sites located within the Coastwide Reference Monitoring System (CRMS;lacoast. gov/crms2) that were classified as either fresh or saline marsh by indicator vegetation species (Visser et al. 1998, Sasser et al. 2014) within Barataria Basin. Coastal wetlands can be classified based on water salinity, elevation, flooding, plant species, or a combination of these variables. Classification systems based on water salinity by Cowardin et al. (1979) and Odum (1984) are commonly used nationwide. Cowardin et al. (1979) noted the years of data needed to estimate average salinity are



Fig. 1 Map of study sites located within Barataria Basin, Louisiana, USA

uncommon and suggested that managers instead use plant species or associations to indicate broad salinity classes. Thus, in practice, the Cowardin et al. (1979) and Odum (1984) systems of classifying marshes by average water salinity have been based on observations of emergent vegetation rather than measurement of water salinity. Establishing sites located at a CRMS site allowed for sites that were independent, and allowed us to easily obtain ancillary ecological data, such as hourly salinity and water-level data. We randomly selected among eight potential sites for a site visit to narrow down site selection. Upon a site visit, we determined whether the following habitat factors were met: 1) presence of openwater habitat (ponding) over 25 m from marsh edge; 2) presence of a continuous, emergent-marsh, edge band at least 25m wide; 3) presence of interior marsh over 25 m from marsh edge. After this evaluation, we selected four sites, two fresh marshes located within the Davis Pond area, and two saline marshes located within the Myrtle Grove area of Barataria Basin. The fresh-marsh study sites were located at CRMS 3166 and 3169 and were comprised of marsh dominated by Sagittaria lancifolia, Colocasia esculenta, or Zizaniopsis milacea. The saline-marsh sites, CRMS 0258 and 0282, were dominated by the saline-tolerant species Spartina alterniflora and Distichlis spicata (Table S4, available online in Supporting Information).

Sample Design

Within each study site, we established 3 study plots (Fig. 2): an emergent-marsh (interior) plot, an edge plot, and an open-water plot. All study plots were 1200 m², measuring 60 m in length and 20 m in depth (Fig. 2). The plots containing marsh edge started 5 m in from the marsh edge and continued out 15 m from marsh edge (Fig. 2). This allowed evaluation of edge use up to 15 m out from the emergent vegetation, 5 m further than previous studies (Sullivan 2015, O'Connell and Nyman 2011), in addition to examination of use at a 5-m emergent-vegetation perimeter. Edge plots were subdivided into 5-m zones. From July 2014 to



Fig. 2 Schematic of study plot design in Barataria Basin, LA, USA, 2014-2015

December 2015, we conducted bird surveys and habitat surveys, and recorded environmental conditions at all study plots. Surveys were conducted at least bimonthly (except December 2014) to observe resident and migratory birds and evaluate seasonal variation in bird use. We sampled 3 microhabitats (emergent, edge, and open water) within each of the 4 selected sites over 10 sample dates, resulting in 120 successful surveys. We considered a sampling survey successful if the bird and habitat surveys were completed on the same day. For each bi-monthly survey, all plots were sampled within the same week.

Bird Surveys

Bird-survey methods were modified from similar studies by O'Connell (2006) and Sullivan (2015) in southwestern Louisiana and the Bird's Foot Delta, respectively. All initial observations were made either from a boat next to a marsh with a camouflage blind material draped over the boat, or, preferentially, from an area of emergent marsh that allowed for inconspicuous observation over the observation interval. For all surveys, we allowed a 15-min settling period after disturbance caused by boat noise and other anthropogenic disturbance. Ideally, all surveys would have occurred in the early morning to capture the maximum number of birds; however, this was not always logistically feasible. Therefore, bird surveys were conducted at varying daylight times. The order of site sampling was rotated to mitigate time-of-day effects (O'Connell 2006, Pickens and King 2014). Due to the inherent patchiness of birds in interior marshes, we conducted 3 consecutive 30-min counts over a 90-min interval (three replicated counts for each sampling trip). This differed slightly from O'Connell (2006) and Sullivan (2015), who both used 15-min counts. Thirty-minute surveys allowed us to minimize counts of zero. To minimize double-counting, surveys were conducted by two observers and birds that were thought to reenter the plots were not counted. Visual observations were made using binoculars and spotting scopes. Additionally, small passerines and secretive marsh birds were often confirmed by their calls. In addition to count data, we recorded the behavior of birds and their distance from the marsh edge (edge plots only). We categorized bird behavior as flush, flyover, forage, loaf, perch, swim, territorial, or vocal. For flyovers, only birds that showed interest in the plot were counted. For example, if a bird only flew over the plot it was not counted; however, a bird that circled the plot multiple times or dipped down to the plot but then flew off was counted and categorized as "flyover".

To increase detection of secretive marsh birds, we conducted a walk-through bird survey at the interior marsh-edge plots and emergent plots. The observer walked diagonally through the entire plot recording any bird that flushed or called and the bird's location within the plot. We used vocal callback surveys for 5 focal secretive marsh-bird species: king rail (*Rallus elegans*), clapper rail (*Rallus crepitans*), sora (*Porzana carolina*), American bittern (*Botaurus lentiginosus*), and common gallinule (*Gallinula galeata*) (Conway 2008, 2011). To avoid inadvertently calling bird into our study plots, we conducted callback surveys at the emergent and marshedge plots after the initial bird-count surveys. At each plot, prior to broadcasting bird calls, we conducted an initial 5-min passive survey in which marsh birds calling prior to callbroadcasts were recorded. After the passive survey segment, we broadcast marsh calls (Sibley's bird call app) for focal bird species for 30 s at a time, with a 5-s pause between each broadcast call (Conway 2011). For maximum effectiveness of the broadcast calls, the speaker was placed upright on the ground and facing center of the marsh when the marsh was not flooded (or just above the water when flooded). The surveyor then stood 2 m to one side of the speaker for the optimal audible range of call backs (Conway 2011).

Habitat and Environmental Variables

After bird surveys were completed, we collected data on thirteen habitat and environmental variables for each sampling survey (Table 1): 1) water temperature (°C), 2) water salinity (ppt), 3) water depth (cm), 4) water depth (cm) at the marsh edge (emergent/open water interface), 5) open water (%), 6) bare ground (%), 7) emergent-vegetation percent cover and species richness, 8) emergent-vegetation structure (visual obstruction/vertical density), 9) SAV percent cover and species richness, 10) floating aquatic vegetation (FAV) percent cover and species richness.

We measured salinity and water temperature with a handheld YSI 63 (Yellow Spring Instruments Inc., Yellow Springs, OH). On 3 days when the YSI was not functioning, salinity and temperature were estimated from the CRMS hourly

 Table 1
 Summary of mean habitat and environmental data (n = 120) (±standard deviation) for all habitat types within Barataria Basin, LA, 2014–2015

| Variable | Fresh Habitat | | | | | Saline Habitat | | | | | | |
|-------------------------------|---------------|-----------|-------|---------|--------|----------------|----------|-----------|-------|---------|--------|-----------|
| | Emergent | | Edge | | Open | | Emergent | | Edge | | Open | |
| water temp (°C) | 21.50 | ±2.1 | 21.50 | ±2.1 | 21.50 | ±2.1 | 24.50 | ±1.3 | 24.50 | ±1.3 | 23.96 | ±2.1 |
| salinity (ppt) | 0.20 | ±0.01 | 0.20 | ±0.01 | 0.20 | ±0.01 | 10.60 | ±0.7 | 10.60 | ±0.7 | 10.63 | ±0.7 |
| water depth (cm) | 9.00 | ±1.7 | 36.50 | ±4.9 | 55.40 | ±5.3 | 2.40 | ±2.4 | 36.50 | ±3.4 | 52.10 | ±5.3 |
| water depth (cm) at edge | n/a | n/a | 21.90 | ±3.2 | n/a | n/a | n/a | n/a | 25.40 | ±3.3 | n/a | n/a |
| open water % | 0.00 | ± 0 | 54.00 | ± 5 | 100.00 | ± 0 | 0.00 | ± 0 | 53.00 | ± 6 | 100.00 | ± 0 |
| bare ground % | 29.00 | ± 4 | 11.00 | ± 4 | 0.00 | ± 0 | 16.00 | ± 4 | 14.00 | ± 4 | 0.00 | ± 0 |
| emergent vegetation % | 70.00 | ±7 | 38.00 | ± 6 | 0.00 | ± 0 | 84.00 | ±5 | 37.00 | ±3 | 0.00 | ± 0 |
| emergent vegetation richness | 3.10 | ±0.4 | 3.20 | ±0.7 | 0.00 | ± 0.0 | 3.10 | ±0.9 | 2.10 | ±0.3 | 0.00 | ± 0.0 |
| emergent vegetation structure | 33.70 | ±3.4 | 28.20 | ±3.6 | 0.00 | ± 0.0 | 36.20 | ±0.6 | 25.80 | ±0.4 | 0.00 | ± 0.0 |
| SAV % | 0.00 | ± 0 | 51.00 | ± 5 | 52.00 | ±7 | 0.00 | ± 0 | 12.00 | ±2 | 6.00 | ± 1 |
| SAV richness | 0.00 | ± 0.0 | 2.60 | ±0.5 | 2.50 | ±0.3 | 0.00 | ± 0.0 | 0.50 | ±0.05 | 0.30 | ±0.03 |
| FAV % | 0.00 | ± 0 | 63.00 | ± 8 | 46.00 | ±7 | 0.00 | ± 0 | 0.00 | ± 0 | 0.00 | ± 0 |
| FAV richness | 1.90 | ±0.2 | 3.20 | ±0.3 | 2.50 | ±0.3 | 0.00 | ± 0.0 | 0.00 | ±0.0 | 0.00 | ± 0.0 |

hydrologic data for those sites. We measured water depth using a meter stick at 12 random points across all zones in open water and marsh edge plots. At every water level point, we measured SAV presence by dipping a 14-tine bow rake to the water bottom and then pulling up; any SAV located on the rake was identified to species and noted as "present" within the plot (Kenow et al. 2006). We recorded any FAV species present at each water level point. Emergent vegetation surveys were conducted using a 4-m^2 quadrat placed at a randomly selected plot pole. Following CRMS protocol (Folse et al. 2012), within the quadrat, we estimated total cover, individual vegetation species, percent cover of each species, dominant species, and the average height. We used an average of Robel measurements taken from the cardinal directions (N, E, W, S) to estimate standing-vegetation density and structure (Robel 1970, Smith 2008) at each point.

Data Analyses

For all analyses, to avoid double counting, we used the maximum number of observations for a bird species during any 30min count interval as the estimate of bird abundance for that species for each survey period (O'Connell and Nyman 2010, 2011). Species and guild richness were defined as the total number of all species and guilds observed during the entire 90-min survey period for a given study plot. We calculated bird density by dividing bird abundance by the total plot area (1200 m²) (O'Connell and Nyman 2010, 2011, Sullivan 2015). Birds are often grouped into foraging guilds when analyzing their habitat use because it can help predict the use of similar species not directly observed. We opted to follow the foraging guild classification used by Sullivan (2015), which closely followed De Graaf et al.'s (1985) classification but is simpler, defining fewer guilds, resulting in less guilds with an observation of zero (Table 2). Furthermore, we preferred this classification scheme because it separated ibises from egrets and herons. These birds are often all grouped together because they are long-legged wading birds though their foraging techniques and preferred prey are different. Therefore, it is likely that their fine-scale habitat needs also differ.

Due to the difficulty of distinguishing the clapper rail and king rail through field observation alone, we classified them according to the salinity type in which they were found. For all observations, the clapper rail was classified for saline habitat, and the king rail was classified for fresh habitat (Maley 2012). The white-faced ibis (*Plegadis chihi*) and glossy ibis (*Plegadis falcinellus*) are also species that are very difficult to distinguish in the field. It was not possible to distinguish between these two species with binoculars alone, especially when either was in juvenile plumage; therefore, we grouped them together as dark ibis (Pickens and King 2014).

We used a hierarchical modeling approach using the lme4 package (Bates et al. 2015) in R (R core team 2017) to create generalized linear mixed-models. Marsh type (fresh or saline), microhabitat (emergent, edge, or open-water), and season (winter, spring, summer, or fall) were included in our models as fixed predictors to explain variability in species (guild)

Table 2 Foraging guild designation for avian species observed in all study plots in Barataria Basin, Louisiana, USA, 2014–2015

| Foraging guild | Guild code | Included species |
|---|------------|---|
| Aerial Insectivores | AI | barn swallow, eastern kingbird, northern rough-winged swallow, purple martin, tree swallow, yellow-billed cuckoo |
| Carnivorous Hawkers and Plungers | CHP | loggerhead shrike, Mississippi kite, northern harrier |
| Dabblers and Grubbers | DG | American coot, black-bellied whistling duck, blue-winged teal, gadwall, green-winged teal, mottled duck |
| Marsh Foragers and Gleaners | MFG | clapper rail, common gallinule, king rail, purple gallinule, sora, Virginia rail, boat-tailed grackle, Carolina wren, clapper rail, marsh wren, red-winged blackbird, savannah sparrow, seaside sparrow, swamp sparrow, white-throated sparrow |
| Mudflat Probers and Gleaners | MPG | dunlin, glossy ibis, killdeer, lesser yellowlegs, roseate spoonbill, white-faced ibis, white ibis, willet |
| Piscivorous Plungers and Divers | PPD | anhinga, belted kingfisher, brown pelican, common tern, double-crested cormorant, Forster's tern, least tern, neotropic cormorant, osprey, royal tern, sandwich tern |
| Scavengers, Food Pirates, and Generalists | SFPG | bald eagle, black vulture, herring gull, laughing gull, turkey vulture |
| Upper Canopy Gleaner | UCG | cedar waxwing |
| Wading Ambusher | WA | black-crowned night heron, great blue heron, great egret, green heron, little blue heron, least bittern, snowy egret, tricolored heron, yellow-crowned night heron |
| Water Bottom Foragers and Divers | WBFD | pied-billed grebe |
| Water Surface Gleaner | WSG | American white pelican |

richness and density. Additionally, zone was added to edgeonly density models to measure the variability in bird density within edge plots associated with distance from marsh edge. Sampling date was added as a random effect to all models to account for variation between dates (i.e., observations made on the same day are more likely to be similar than observations within the same season made on a different day). Our models had a negative binomial distribution ---to account for overdispersion in the Poisson models-with a log link function. For model selection, we used estimates of maximum likelihood with a Laplacian approximation for small sample size (Zar 2010). We used Akaike's second-order information criterion (AIC_c) to rank and select the best fit models with the fewest parameters (lowest AIC_c) for each response variable (Burnham and Anderson 2002). This is a second-order variant that accounts for small sample size by adding an additional bias-correction term to avoid overfitting the models. All models with $\Delta AIC_c < 4$ indicate substantial empirical support for the model (Burnham and Anderson 2002); therefore, we only retained models with $\Delta AIC_c < 4$.

We ran a canonical correspondence analysis (CCA) using the vegan (Oksanen et al. 2017) package in R (R core team 2017) to identify species (guild) associations with environmental variables. We used Monte Carlo permutation (999 permutations) tests with forward selection to measure the significance of environmental variables on species (guild) composition, and to select the model that best explained variability. We $\log (x + 1)$ transformed environmental variables due to difference in scales of measurement among the variables. Depth at marsh edge was excluded from the analysis because it was only measured at marsh-edge plots. Rare (observed <1%) bird species and guilds (observed <5%) were not included in this CCA. Prior to the CCA, a multiple regression was run using car (Fox and Weisberg 2011) and MASS (Venables and Ripley 2002) packages in R (R core team 2017) to check for issues due to multicollinearity between variables. For variables that demonstrated high collinearity (>0.75) and for which one variable could explain the variation, we reduced them to one variable. The variables FAV percent cover, SAV percent cover, FAV species richness, and SAV species richness were all highly correlated, so we reduced them to the variable "aquatic vegetation". The variables emergentvegetation richness, percent cover, and structure were all highly correlated, so we reduced them to the variable "emergent vegetation".

Results

During the study, we conducted 120 successful surveys and identified 1117 birds of 68 bird species comprising 11 guilds (Table 3, Table S1, available online in Supporting Information). Overall, fresh marsh had approximately 2.6 times as many birds as saline marsh. Fresh-marsh edge plots had the highest relative abundance (0.39), followed by fresh-marsh emergent (0.19) and saline-marsh edge plots (0.17) (Table 3, S1). The red-winged blackbird had the highest relative abundance (0.23), followed by the boat-tailed grackle (0.07), common gallinule (0.06), barn swallow (0.06), and blue-winged teal (0.05) (Table 3). Marsh foragers and gleaners was the guild with the highest relative abundance (0.48), followed by aerial insectivores (0.12), wading ambushers (0.10), dabblers and grubbers (0.09), and mudflat probers and gleaners (0.09) (Table 4).

Species and Guild Richness

Models indicated that marsh type and microhabitat were the predictors that best explained variation in species richness, with microhabitat being the most parsimonious model (Table 5). Similarly, microhabitat was the best predictor for guild richness. Richness was greatest at edge plots for species (mu = 4.82 ± 0.15 SE) and guild (mu = 3.56 ± 0.09 SE) (Fig. 3).

Wetland Bird Density

Models indicated that the interaction of marsh type and microhabitat best explained variation in wetland-bird density (birds ha⁻¹) (Table 5). Because red-winged blackbirds accounted for nearly a quarter (23%) of birds counted, we examined models of density with and without red-winged blackbirds. Wetland-bird density in which red-winged blackbirds were included, was greatest at fresh-marsh edge plots $(mu = 172.24 \pm 0.24 \text{ SE})$ (Fig. 3c). Within open-water microhabitats, wetland-bird density varied slightly between open water in fresh marsh (mu = 49.13 ± 0.22 SE) and open water in saline marsh (mu = 34.93 ± 0.21 SE) (Fig. 3c). For wetlandbird density without red-winged blackbirds, the interaction of marsh type and microhabitat best explained variation (Table 5). The same trends remained with bird density greatest at fresh-marsh edge microhabitats (mu = 124.00 ± 0.23 SE) (Fig. 3d). Within open-water microhabitat, bird density did not vary between open water in fresh marsh (mu = $39.93 \pm$ 0.23 SE) and open water in saline marsh (mu = 35.01 ± 0.23 SE) (Fig. 3d).

Within Edge Effects

Models indicated that zone was a good predictor of bird density when the interaction of marsh type was present (Table 5). At fresh-marsh edge plots, the greatest density (mu = 187.78 \pm 0.21 SE), was at the edge (0–5 m range). At saline-marsh edge plots, the greatest density mu = 58.16 \pm 0.22 SE) was at the 5–10 m range (Fig. 4). Within both marsh types, densities

| Species Common Name | Species Scientific Name | Species Code | All Habitats | Fresh Habitat | | Saline Habitat | | | |
|-------------------------------|----------------------------|--------------|--------------|---------------|-------|----------------|----------|-------|-------|
| | | | | Emergent | Edge | Open | Emergent | Edge | Open |
| red-winged blackbird | Agelaius phoeniceus | RWBL | 0.234 | 0.335 | 0.255 | 0.177 | 0.333 | 0.190 | 0.000 |
| boat-tailed grackle | Quiscalus major | BTGR | 0.072 | 0.094 | 0.105 | 0.056 | 0.063 | 0.016 | 0.000 |
| common gallinule | Gallinula galeata | COGA | 0.060 | 0.090 | 0.103 | 0.024 | 0.000 | 0.000 | 0.000 |
| barn swallow | Hirundo rustica | BARS | 0.057 | 0.094 | 0.071 | 0.024 | 0.000 | 0.043 | 0.011 |
| blue-winged teal | Anas discors | BWTE | 0.045 | 0.009 | 0.014 | 0.153 | 0.000 | 0.071 | 0.109 |
| white ibis | Eudocimus albus | WHIB | 0.045 | 0.080 | 0.064 | 0.032 | 0.000 | 0.005 | 0.000 |
| great egret | Ardea alba | GREG | 0.044 | 0.000 | 0.030 | 0.065 | 0.048 | 0.087 | 0.098 |
| seaside sparrow | Ammodramus maritimus | SESP | 0.034 | 0.000 | 0.000 | 0.000 | 0.238 | 0.114 | 0.022 |
| black-necked stilt | Himantopus mexicanus | BNST | 0.031 | 0.052 | 0.039 | 0.048 | 0.000 | 0.000 | 0.000 |
| tree swallow | Tachycineta bicolor | TRES | 0.028 | 0.028 | 0.039 | 0.000 | 0.000 | 0.043 | 0.000 |
| American coot | Fulica americana | AMCO | 0.024 | 0.000 | 0.014 | 0.129 | 0.000 | 0.000 | 0.054 |
| dark ibis* | Plegadis sp. | DAIB | 0.024 | 0.042 | 0.032 | 0.032 | 0.000 | 0.000 | 0.000 |
| Mississippi kite | Ictinia mississippiensis | MIKI | 0.024 | 0.000 | 0.059 | 0.008 | 0.000 | 0.000 | 0.000 |
| snowy egret | Egretta thula | SNEG | 0.024 | 0.014 | 0.014 | 0.065 | 0.016 | 0.022 | 0.054 |
| northern rough-winged swallow | Stelgidopteryx serripennis | NRWS | 0.018 | 0.028 | 0.032 | 0.000 | 0.000 | 0.000 | 0.000 |
| double-crested cormorant | Phalacrocorax auritus | DCCO | 0.014 | 0.000 | 0.000 | 0.032 | 0.032 | 0.027 | 0.054 |
| clapper rail | Rallus crepitans | CLRA | 0.013 | 0.000 | 0.000 | 0.000 | 0.111 | 0.038 | 0.000 |
| Forster's tern | Sterna forsteri | FOTE | 0.012 | 0.000 | 0.005 | 0.000 | 0.000 | 0.043 | 0.033 |
| tricolored heron | Egretta tricolor | TRHE | 0.012 | 0.005 | 0.002 | 0.040 | 0.000 | 0.011 | 0.043 |

Table 3Relative abundances within marsh type and microhabitat type of the 19 most abundant waterbird species, of 68 waterbird species observed, atsurveyed plots in Barataria Basin, LA, USA, 2014–2015. Four-letter alpha code for species names (Pyle and DeSante 2014)

*Dark ibis includes both the white-faced (*Plegadis chihi*) and glossy ibis (*Plegadis falcinellus*) due to difficulty distinguishing them in the field. Only the most abundant species are listed here. For all species relative abundances, see Table S1.

did not diminish with distance from marsh edge up to 15 m; therefore, the edge effect for wetland birds extends at least

15 m out from the emergent/open-water interface (edge) within both marsh types.

Table 4Relative abundances within marsh type and microhabitat type of 12 waterbird guilds observed at surveyed plots in Barataria Basin, LA, USA,2014–2015

| Guild | Guild Code | All Habitats | Fresh Habitat | | | Saline Habitat | | |
|---|------------|--------------|---------------|-------|-------|----------------|-------|-------|
| | | | Emergent | Edge | Open | Emergent | Edge | Open |
| Marsh Foragers and Gleaners | MFG | 0.482 | 0.120 | 0.217 | 0.038 | 0.043 | 0.063 | 0.003 |
| Aerial Insectivore | AI | 0.107 | 0.030 | 0.057 | 0.003 | 0.000 | 0.017 | 0.001 |
| Wading Ambusher | WA | 0.104 | 0.006 | 0.022 | 0.021 | 0.004 | 0.023 | 0.027 |
| Dabblers and Grubbers | DG | 0.088 | 0.002 | 0.021 | 0.036 | 0.000 | 0.012 | 0.018 |
| Mudflat Probers and Gleaners | MPG | 0.085 | 0.027 | 0.038 | 0.008 | 0.001 | 0.009 | 0.004 |
| Piscivorous Plungers and Divers | PPD | 0.059 | 0.000 | 0.006 | 0.004 | 0.002 | 0.027 | 0.020 |
| Scavengers, Food Pirates, and Generalists | SFPG | 0.035 | 0.002 | 0.004 | 0.004 | 0.006 | 0.009 | 0.015 |
| Carnivorous Hawkers and Plungers | CHP | 0.030 | 0.003 | 0.024 | 0.001 | 0.000 | 0.002 | 0.000 |
| Water Surface Gleaner | WSG | 0.005 | 0.000 | 0.000 | 0.000 | 0.000 | 0.003 | 0.003 |
| Upper Canopy Gleaner | UCG | 0.004 | 0.001 | 0.003 | 0.000 | 0.000 | 0.000 | 0.000 |
| Water Bottom Foragers and Divers | WBFD | 0.002 | 0.000 | 0.000 | 0.000 | 0.000 | 0.001 | 0.001 |
| | | Totals | 0.191 | 0.392 | 0.115 | 0.056 | 0.166 | 0.092 |

| Table 5 Model selection explaining habitat use of | Response variable | Models | k | AICc | ΔAICc | wiAICc |
|---|---------------------|--|----|---------|-------|--------|
| waterbirds in Barataria Basin, LA, USA, 2014–2015. Variables | Species Richness | Microhabitat + (1 Date) (1.75) | 6 | 524.68 | 0.00 | 0.51 |
| included in the models were | • | SalHabitat:MicroHabitat+(1 Date) (2.93) | 9 | 527.03 | 2.35 | 0.16 |
| Salhabitat (fresh and saline); | Guild Richness | Microhabitat + $(1 Date)$ (1.30) | 6 | 428.91 | 0.00 | 0.72 |
| Microhabitat (emergent | | SalHabitat:MicroHabitat+ (1 Date) (1.34) | 9 | 431.96 | 3.05 | 0.16 |
| Zone (distance from marsh edge); Date (Sampling date). parameter (dispersion parameter) | Density (all) | SalHabitat:MicroHabitat+ (1 Date) (1.35) | 9 | 1257.22 | 0.00 | 0.92 |
| | Density (w/o RWBL) | SalHabitat:Microhabitat+ (1 Date) (1.29) | 9 | 1200.53 | 0.00 | 0.87 |
| | Density (edge only) | SalHabitat+ (1 Date) (1.29) | 4 | 856.00 | 0.00 | 0.75 |
| | | SalHabitat:Zone+(1 Date) (1.32) | 10 | 859.36 | 3.36 | 0.14 |

SalHabitat:Season+(1|Date) (1.24)

Environmental Effects

Monte Carlo models showed that the environmental variables that best explained species composition were salinity, open water, emergent vegetation, water temperature, and aquatic vegetation (Table S2, available online in Supporting Information). The first two canonical axes explained 77% of

the species-environmental variation. Axis 1 explained 49% of variation in species abundance and represented the gradient from highly saline habitats devoid of aquatic vegetation to habitats with more aquatic vegetation with lower salinities. Axis 2 explained 28% of the variation in species abundance and represented the gradient from open water communities with lower temperatures to emergent vegetation communities

10

859.96

3.96

0.10



Fig. 3 Mean species richness (±standard error) (a), mean guild richness (±standard error) (b), and mean waterbird density with red-winged blackbirds (c) and without red-winged blackbirds (d) for microhabitats and marsh types in Barataria Basin, LA, USA, 2014 and 2015



Fig. 4 Mean bird count (\pm standard error) at edge plot subdivisions in Barataria Basin, LA, USA 2014–2015

with higher temperatures. Both axes were related to vegetation, but different bird species were associated with different types of vegetation.

Many species were associated with more complex vegetation communities (i.e., emergent, and aquatic vegetation) (Fig. 5a). The northern rough-winged swallow, boat-tailed grackle, tree swallow, and red-winged blackbird were associated with emergent vegetation community structure. The white ibis, dark ibis, common gallinule, and black-necked stilt all showed an association with aquatic vegetation. Conversely, there were species that showed strong associations with less complex vegetation communities and a higher availability of open water. The American coot, laughing gull, blue-winged teal, and great egret were all associated with areas of greater open water. The least tern, seaside sparrow,



Fig. 5 Canonical correspondence tri-plot relating waterbird a) species and b) guilds to environmental variables in Barataria Basin, LA, USA, 2014–2015. The orientation of each variable in relation to the axes 1 and 2

clapper rail, and Forster's tern were associated with higher salinities and water temperatures.

Monte Carlo models showed that the environmental variables that best explained guild-composition variability were salinity, depth, emergent vegetation, and water temperature (Table S3, available online in Supporting Information). The first two canonical axes explained 91% of the speciesenvironmental variation. Axis 1 explained 71% of variation in guild abundance and represented the gradient from highly saline habitats to lower salinities. Axis 2 explained 20% of the variation in guild abundance and represented the gradient from deeper water communities and lower temperatures to emergent vegetation communities and higher temperatures.

Foraging guilds showed little overlap in environmental variable associations because they were grouped by ecological niche (Fig. 5b). The aerial insectivores and marsh foragers and gleaners were associated with emergent vegetation. Dabblers and grubbers were associated with increasing water depth. Piscivorous plungers and divers, and wading ambushers were associated with higher salinities while mudflat probers and gleaners were associated with lower salinities.

Species of Concern

We observed nine species of concern from Louisiana's 2014 Watch List (Rosenberg et al. 2014). The mottled duck (n = 10) was the only species observed from the Red Watch List. Species from the Yellow Watch List included the king rail (n = 4), lesser yellowlegs (n = 4), willet (n = 6), and dunlin (n = 1). Additionally, common species in steep decline included the purple gallinule (n = 3), herring gull (n = 1), yellow-billed cuckoo (n = 3), and loggerhead shrike (n = 2). The total number of birds (n = 34) that belonged to the species of concern, or species in steep decline, was too low for statistical analysis (Table S1, available online in Supporting Information).



is represented by the arrows; the length indicates the degree of correlation to the axes. Additional supporting information may be found in the online version of this article at the publisher's website.

Discussion

Edge microhabitats supported greater bird species and guild richness when compared to open-water and emergent microhabitats, regardless of season and marsh type. The presence of a more complex vegetation community at edge microhabitats likely increased niche availability, supporting greater richness. Specifically, emergent vegetation and SAV were present at all edge plots, with FAV present in fresh marsh edge habitat. In contrast, open water microhabitats lacked emergent vegetation, while emergent microhabitats lacked SAV and FAV. This diversity of vegetation structure in edge plots likely provided an increase in refuge and foraging potential for birds. Furthermore, bird species richness was lowest in saline marsh emergent vegetation plots and this was likely due to the absence of SAV and FAV that resulted in a less complex (layered) community.

Marsh habitats providing increased diversity and amount of refuge and foraging habitat, as indicated by greater vegetation diversity (i.e., SAV, FAV, emergent marsh) supported greater bird density. For example, fresh-marsh emergent and edge microhabitats supported greater wetland bird density compared to saline-marsh emergent and edge habitat, regardless of season; these fresh-marsh habitats were characterized by both SAV and FAV, unlike their saline counterparts. These observations that birds were more abundant in fresh marshes than in saline marshes also agrees with Palmisano (1973), who found greater waterfowl abundance in fresh marshes than in saline marshes within coastal Louisiana. Similarly, bird density did not vary by marsh type for open-water microhabitats; instead, densities in open water were similar regardless of salinity type or season. The consistency of bird density at open water plots regardless of marsh type and season is most likely attributed to the fact that open water microhabitats in both marsh types similarly provided no refuge for birds but did provide beneficial foraging for certain bird species (e.g., dabblers and grubbers; piscivorous plungers and divers; and wading ambushers) (Pearse et al. 2012). Within emergent and edge microhabitats, the amount and diversity of refuge and foraging habitat varied between salinity types, and bird density differed.

An edge effect of enhanced bird abundance at all edge habitats compared to open water was evident. This is highlighted by quantifying the edge effect as the ratio of number of birds in edge habitat compared to open water. Across all seasons, the edge effect was approximately 3.5:1in fresh marsh and 2:1in saline marsh. O'Connell and Nyman (2010) found that the edge effect for wetland birds within brackish marshes was 2.8:1, which is between our estimates in fresh marsh and saline marsh. Edge effects in our study extended to at least 15 m out from the marsh edge. This differs from past studies in south Louisiana that assumed that the edge effect is limited to open water within 0–10 m of emergent vegetation

(Sullivan 2015, O'Connell and Nyman 2010). In fresh habitat, this large edge effect might partially be explained by birds often using thick floating mats of Eichhornia crassipes (often seen during site visits at fresh habitat sites) to extend their foraging range. Within saline communities, this effect may be reduced relative to freshwater communities because edges in saline waters are more tidally influenced and thus impeded access to more prey items for foraging birds. Piscivorous plungers and divers were often seen foraging in the distal zone of the marsh edge. Baltz et al. (1993) concluded that the edge effect was limited to within 7 m of emergent vegetation, with the first 1.25 m of marsh edge most productive for nekton. However, throw-trap sampling generally fails to collect benthic organisms, and small crustaceans that can bury in the mud (Turner and Trexler 1997). Thus, foraging piscivorous plunging and diving birds may be a better indicator of nekton presence.

Regardless of marsh type or season, edge habitat at our sites supported 1.8 times more species and guild richness than did emergent and open water habitats. Concordant with these findings, Weller and Spatcher (1965) found that species richness and abundance generally decrease with increasing open water, but the abundance of some swimming species may increase. Weller and Spatcher (1965) modeled the habitat cycle of semi-permanent marshes in the Midwestern glacial pothole region, which closely mimics the succession of marsh degradation of Louisiana marshes. If marsh degradation continues at its anticipated rate, the shifts in marsh communities will cause the abundance of some species to increase while others will decrease. The abundance of species that associate with open water (e.g., dabblers and grubbers, wading ambushers, piscivorous plungers and divers) would likely increase, while numbers of most other species (e.g., marsh foragers and gleaners, aerial insectivores, mudflat probers and gleaners) associated with emergent vegetation would decrease (Weller and Spatcher 1965, Fairbairn and Dinsmore 2001).

Water depth, along with salinity, emergent vegetation, and water temperature affected guild composition variability, but not species composition. Water depth is often cited as one of the main drivers and limiting factors in bird use of coastal habitats (Bancroft et al. 2002, Lantz et al. 2010, Rajpar and Zakaria 2011). Our results were similar to those of Esters (1986) who found significant correlations between use by mottled ducks and areas of open water habitat in Louisiana but did not find significant relationships between use by mottled ducks and overall water depth. We also found that emergent structures were strong predictors of species composition, as was aquatic vegetation when paired with salinity. Pearse et al. (2012) found that diversity of habitat was an important factor in waterfowl abundance. It may be that water depth was confounded with the emergent and aquatic vegetation communities, thus indirectly driving bird use.

It is important to note that much of our analyses were driven by the 19 bird species that made up 99% of all the birds observed, and that the waterfowl estimates may be low due to their wariness. While our findings suggest that understanding the use of microhabitats by birds at finer scales may be critical for management and restoration, our study took place on a small scale within one hydrologic basin. A similar study at a larger scale, across multiple basins would build upon our findings and provide additional insights on managing birds across the landscape and making predictions coastwide in Louisiana. For instance, a study that extends across all salinity regimes in coastal Louisiana would increase our understanding of bird habitat use in the transitional area between intermediate and brackish marshes, both of which are dominated by Spartina patens in Louisiana. Furthermore, examining the extent of marsh edge use past the 15-m range could further refine the threshold of bird use from the edge. Particularly in saline habitats, examining the influence of tides on the edge use, which we were unable to survey, would increase our understanding of bird use at varying water levels.

This study is the first to compare bird use among edge, open-water, and interior emergent habitats across an estuarine gradient. These parameters provide insights on bird use of specific habitats and will help biologists and managers predict the potential effects on birds of habitat conversion from emergent marsh to open water in Louisiana. Finer-scale environmental characteristics that were found to explain bird use may also be useful to restoration planners who wish to assess and compare the effects of potential marsh restoration projects on birds. By investigating the effects of a comprehensive set of spatial, temporal, and environmental parameters on birdhabitat use within Louisiana coastal marshes, we found that the associations between birds and these parameters are complex. Factors such as marsh edge, salinity, aquatic and emergent plants, and open-water availability were all strongly related to habitat use by birds. Overall, edge habitats in freshwater supported the highest density and richness of bird species and guilds. However, both fresh and saline conditions provided beneficial habitat for birds and there were species that were unique to each salinity type. As sea level rises, freshwater flows change, and managers seek to respond and adapt to these shifts, understanding bird habitat associations will be useful in attempts to predict the effects of marsh loss, salinity changes, and restoration on habitat quality for birds in coastal Louisiana and other coastal areas.

Conclusions

Coastal marshes are expected to continue to decline in extent because of development and sea-level rise (Dahl 2011). Our data provide a basis for estimating how bird density might be affected by changes in marsh area and type. Future management and coastal restoration that increases edge habitat and maximizes emergent vegetation habitat and fresh marshes would likely enhance bird richness and density across coastal Louisiana. Fine-scale landscape patterns provide beneficial habitat features to support a rich and abundant bird community and are critical components of restoration and management planning. Future modelling efforts for Barataria Basin would likely be improved from the assumption that the marsh edge effect for birds extends 20 m from emergent vegetation into open water and that the edge effect enhances bird densities from 3.5 in fresh marsh to 2.0 in saline marsh.

Acknowledgments We thank S. Piazza, B. Bechnel, K. DeMarco, E. Hillman, L. Sullivan, C. Hall, and C. Flucke for assistance with data collection and logistics. R. Villani and two anonymous reviewers provided valuable comments on a previous version of this manuscript. Additionally, we thank K. Ringelman and S. King for useful comments and recommendations throughout this study. Funding to support this work came from the Gulf Coast Prairie Landscape Conservation Cooperative, U.S. Fish and Wildlife Region 2 and Region 4 (SSP funding). Data published in Patton (2016). Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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