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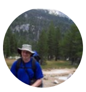

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14 PUBLICATIONS **52** CITATIONS

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65 PUBLICATIONS **503** CITATIONS

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Multiscale Habitat Selection of Wetland Birds in the Northern Gulf Coast

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Abstract The spatial scale of habitat selection has become a prominent concept in ecology, but has received less attention in coastal ecology. In coastal marshes, broad-scale marsh types are defined by vegetation composition over thousands of hectares, water-level management is applied over hundreds of hectares, and fine-scale habitat is depicted by tens of meters. Individually, these scales are known to affect wetland fauna, but studies have not examined all three spatial scales simultaneously. We investigated wetland bird habitat selection at the three scales and compared single- and multiscale models. From 2009 to 2011, we surveyed marsh birds (i.e., Rallidae, bitterns, grebes), shorebirds, and wading birds in fresh and intermediate (oligohaline) coastal marsh in Louisiana and Texas, USA. Within each year, six repeated surveys of wintering, resident, and migratory breeding birds were conducted at >100 points (n=304). The results revealed fine-scale factors, primarily water depth, were consistently better predictors than marsh type or management. However, 10 of 11 species had improved models with the three scales combined. Birds with a linear association with water depth were, correspondingly, most abundant with deeper fresh marsh and permanently impounded water. Conversely, intermediate marsh had a greater abundance of shallow water species, such as king rail *Rallus elegans*, least bittern *Ixobrychus exilis*, and sora *Porzana carolina*. These birds had quadratic relationships with water depth or no relationship. Overall, coastal birds were influenced by multiple scales corresponding with hydrological characteristics. The effects suggest the timing of drawdowns and interannual variability in spring water levels can greatly affect wetland bird abundance.

Keywords Drawdown · Marsh birds · Marsh management · Rallidae · Spatial scale · Water depth

Introduction

The influence of spatial scale on animal distribution and habitat use is prominent in ecology (Wiens 1989), but has received less attention in coastal ecology. The fauna of coastal wetlands, including fish, shrimp, crabs, shellfish, alligators, ducks, and a diverse assemblage of resident and migratory birds, give coastal wetlands an extremely high socioeconomic (Costanza et al. 1989) and ecological value (Lotze et al. 2006; Mitsch and Gosselink 2007). Coastal wetlands in the eastern USA are particularly important as they represent 38 % (16.1 million ha) of the total wetlands in the USA (Stedman and Dahl 2008). With threats to coastal wetlands expected to increase due to increasing storm effects, urbanization, and sea-level rise, management will need to effectively operate at a scale appropriate for fauna. Nonetheless, few studies have explicitly compared the spatial scale of fauna habitat relationships in coastal marsh. Rozas and Minello (2010) have shown nekton to be related to a hierarchy of marsh type, pond size, and to a lesser degree, water depth. For coastal bird populations, studies have assessed marsh types and management (Gabrey et al. 2001; Fitzsimmons et al. 2012) or fine-scale marsh characteristics (Rush et al. 2009), but research has not simultaneously compared all three spatial scales.

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Broad-scale marsh types are defined by dominant vegetation species along flooding and salinity zones (freshwater, intermediate, brackish, saline). Research on fauna distribution among marsh types has generally focused on nekton with prominent differences among marsh types (Rozas and Minello 2010) and with salinity thresholds (King et al. 2005; Greenwood 2007). The effect of marsh type on terrestrial fauna is less well known, and the few demonstrated differences are difficult to interpret because of complex management interactions and yearly changes in animal abundance (Gabrey et al. 2001; Fitzsimmons et al. 2012). Within marsh types, water-level management is conducted by natural resource agencies and private landowners, or may be dictated by historical land uses. Marsh impoundments are common and can include levees and water pumps used with structural marsh management (Montague et al. 1987; Cowan et al. 1988). The objectives of water-level management can vary greatly (see Cowan et al. 1988; Mitchell et al. 2006). Our study sites aimed to manage for fish and wildlife (particularly winter waterfowl habitat), produce annual plants for wintering waterfowl, and mitigate human modifications to water flow; management was limited at a few sites due to levees constructed prior to public ownership. The negative effects of impoundments (e.g., Rogers et al. 1994; Bryant and Chabreck 1998) should always be considered by wetland managers, but here, we focused on how medium-scale water level manipulations affected wintering, breeding resident, and migratory breeding birds. Within marsh types and management regimes, fine-scale bird habitat features include water depth, vegetation structure, and open water; these conditions vary temporally with weather conditions, disturbance events, microtopography, and vegetation composition.

In this study, we were interested in a wide-ranging suite of wetland birds, but marsh birds (i.e., Rallidae, bitterns, grebes) were of primary interest because of their conservation status worldwide (Pacheco and McGregor 2004; Poulin et al. 2009), conservation concerns in the continental USA (Conway 2011), and the fundamental lack of knowledge about coastal populations. The king rail *Rallus elegans* is a conservation priority for the US Fish and Wildlife Service because of its recent decline (Cooper 2008), and migratory species, such as the purple gallinule *Porphyrio martinicus*, are widespread in the Americas, yet little is known of their habitat use. Marsh bird research has examined local habitat, such as open water-vegetation edges or vegetation composition (Conway and Sulzman 2007; Rush et al. 2009) as well as broader landscape variables such as wetland area (Naugle et al. 1999), tree cover (Pickens and King 2012), and open water-vegetation interspersion at a 5-km scale (Rehm and Baldassarre 2007). However, the effects of marsh type, hydrological management regimes, and an array of fine-scale habitat characteristics are relatively unknown for marsh birds.

We investigated multiscale habitat selection of wetland birds in the Gulf Coast marshes of Louisiana and Texas, USA. At the broadest scale, fresh and intermediate (oligohaline) marsh types encompassed tens of thousands of hectares. Water-level management was a medium-scale factor, which determined the depth, duration, and seasonality of flooding over hundreds of hectares. At a fine-scale, habitat was investigated within 100 m of bird survey points. The objectives of our research were to (1) determine fine-, medium-, and broad-scale factors affecting habitat selection of marsh bird, shorebird, and wading bird species; (2) determine the spatial scale that best correlates with wetland bird habitat selection; and (3) compare single-scale habitat models with multiscale models. Based on the multiscale character of wetland flooding, we hypothesized wetland bird habitat selection would be best explained by a combination of the three spatial scales compared to any single scale.

Methods

Study Area

Study sites were in the Chenier Plain coastal region of Louisiana and Texas, USA (Fig. 1). The Cheniers, or sand ridges, have an origin from sediment deposition and the reworking of sediments (Penland and Suter 1989), and the ridges restrict tidal action. Water levels are primarily determined by rainfall, seasonal wind-driven tides, and management. Rainfall from November to February typically floods emergent marsh vegetation, and then marshes dry by April–June except for permanent ponds, canals or ditches, and impoundments. Water flow in the region has been modified by channels, levees, and water control structures to prevent salinity intrusion and for rice agriculture to the north (Gunter and Shell 1958). We used the definition of fresh and intermediate (oligohaline) marshes as described by Visser et al. (2000). Fresh marshes were dominated by *Panicum hemitomon*, *Typha* spp., and *Sagittaria lancifolia*, while intermediate marshes were dominated by *Spartina patens*, *Phragmites australis*, *Schoenoplectus* spp., *Typha* spp., and *Paspalum vaginatum*. Fresh marsh sites included Lacassine National Wildlife Refuge (NWR), White Lake Wetlands Conservation Area, and most of Cameron Prairie NWR. Intermediate marsh sites included McFaddin NWR, Anahuac NWR, J.D. Murphree Wildlife Management Area, Rockefeller State Wildlife Refuge, and part of Cameron Prairie NWR.

Wetland Bird Surveys

Bird surveys were conducted March 9–June 19 from 2009 to 2011, and surveys included wintering, resident breeding, and

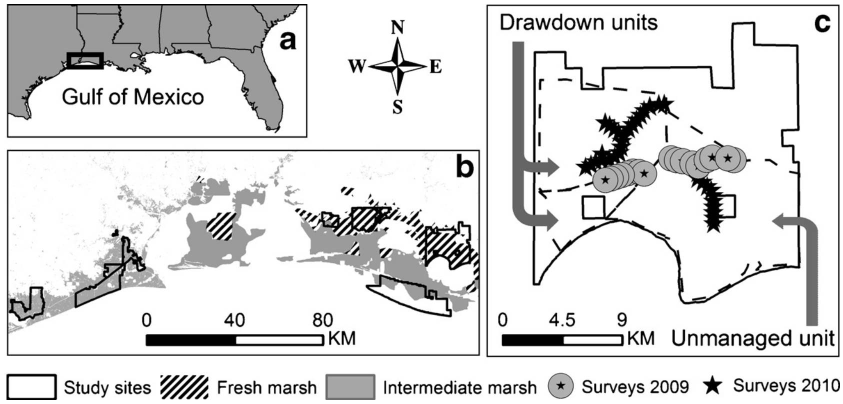


Fig. 1 **a** Extent of study area in northern Gulf Coast; **b** study sites in Louisiana and Texas, USA, with marsh types symbolized; **c** example of bird survey locations in drawdown and unmanaged management types (*dashed lines*) in White Lake Wetlands Conservation Area

migratory breeding birds. March coincided with the beginning of the resident breeding season, and all birds became quiet by mid-June. Approximately ten survey points were placed along transects with ≥400 m between points in 2009 and 2010 when travel was conducted by vehicle (Fig. 1). In 2011, interior survey points were conducted, which were spaced by ≥200 m as travel was by foot; 6–8 points were on each transect. Interior surveys were ≥250 m from levees or ditches, and transects were placed in areas that had high habitat variability among points according to a concurrent remote sensing study (Pickens 2012). A total of 17 transects were in fresh marsh (n=130), and 18 transects were in intermediate marsh (n= 174). Bird survey points in Texas sites were replicated in 2009 and 2010 to quantify temporal variation in species abundances. Each survey point was marked to maintain a consistent survey location, and six surveys were performed at each point annually.

We used a call-back survey technique as described by Conway (2011), since marsh bird studies have shown the technique is superior to passive surveying (see Conway and Gibbs 2011 for a review). Surveys were conducted 30 min before sunrise until 4 h after sunrise, and surveys were not conducted during rainfall or with winds >20 km/h. The order of survey points along each transect was consistently changed to ensure any time of day effect was negligible. Surveys were conducted on one side of the marsh (i.e., 180° semicircle) by auditory and visual observation for 5 min during a passive period. Then an MP3 player and 80–90-dB speakers (at 1 m) played 30 s of marsh bird calls followed by 30 s of silence. Calls of black rail *Laterallus jamaicensis*, American bittern *Botaurus lentiginosus*, least bittern *Ixobrychus exilis*, common gallinule *Gallinula galeata*, king rail, purple gallinule, and pied-billed grebe *Podilymbus podiceps* were played in that order. Distances to birds were recorded to the nearest 10 m. Nine observers surveyed birds from 2009 to 2011 with one observer surveying for all 3 years. Within each year, observers were rotated on transects to minimize observer bias. At least 2 weeks of intensive training was used annually to train observers to identify species and estimate distance to birds. We classified the two species of *Plegadis* spp. into a single category of dark ibis; greater and lesser yellowlegs *Tringa* spp. were also classified into a single category. Ducks were not counted during surveys due to their brief residence during the study period, but all other waterbirds were recorded. King rail and clapper rail *Rallus longirostris* may hybridize in brackish marsh (Meanley 1969), but tidal creeks and daily tidal inundation, which are commonly associated with clapper rails, were not present at the intermediate marsh sites. Therefore, all *Rallus* were considered king rail.

Classification of Management Type

Throughout the study, a variety of management types were surveyed in fresh and intermediate marshes. The study was designed to survey multiple management types within each site (e.g., Fig. 1) or with adjacent sites. Impoundments varied from structures that held water throughout the year to impoundments where water was drawn down beginning from late March to mid-May. The former was classified as "permanently impounded water" and the latter as "drawdown" according to their typical management. Marshes with permanently impounded water were usually former rice fields with levees preventing drainage. We did not survey the few areas in intermediate marsh where water was held at a shallow level (i.e., <10 cm) for the breeding bird season. "Unmanaged" marsh was defined as areas where direct water manipulation or impoundment was absent. Drawdown marshes varied in their duration of flooding and timing of drawdown, but all of these marshes held water levels relatively deep (>20 cm) throughout the fall and winter to provide habitat for waterfowl and other wintering birds. White Lake and Rockefeller were drawn down in mid-May while JD Murphree typically draws down water levels beginning in late March. Managed marsh differed with annual conditions and decision making by managers, but we were concerned with overall differences in managed and unmanaged marshes. Storm surge from Hurricane Ike in the fall of 2008 changed management strategies for spring 2009. For instance, JD Murphree received saline storm surge in their impoundments. To dilute the salt in the marsh impoundments, rainfall and water from the adjacent bayou were held in the impoundments later in the season compared to typical years. In 2011, JD Murphree had drought conditions, and a drawdown was not conducted. These annual distinctions were accounted for with fine-scale habitat characteristics.

Fine-Scale Habitat

Fine-scale habitat measures included percent open water, water depth, length of open water-vegetation edge, presence of a ditch, and a vegetation density index. Between March 25 and April 18 of each year, water depth was measured at each bird survey point. The measurements occurred after the second round of bird surveys, coincided with resident bird nesting and peak calling of wintering birds, and directly preceded the arrival of breeding migratory birds. Wintering shorebirds and resident wading birds were primarily recorded in this early season as well. At each bird survey point, water depth was recorded every 10 m along three 50-m transects (5 points/transect=15 depth measurements). One transect was perpendicular to the survey point, and two transects were at ~20° angles from the point. No water depths were measured ≤10 m from levees or ditches; transects were extended when levees or ditches impeded measurements. Deep ditches (>50 cm) were not measured because ditches were accounted for elsewhere (see below). Mean water depths from the three transects were calculated for each survey point.

From late April to early May, three vegetation surveys were conducted at each bird survey point. Vegetation surveys corresponded to water depth transects, and surveys were conducted 30 m along each transect. Within a 10-m radius (0.03 ha) of each vegetation survey point, the percent of open water was recorded. As an index of vegetation density, a Robel pole was used at each point to measure the visual obstruction of vegetation (Robel et al. 1970). Two measures were taken and averaged together; measurements were recorded at a 1-m height at a distance of 2 m from the pole. During vegetation surveys, we sketched open water and emergent vegetation within a 100-m radius of each bird survey point's semicircle. Sketches were later transferred to ArcGIS 9.3 (ESRI, Redwoods, CA) at a 5-m spatial resolution, and open water-vegetation edge (meters per hectare) was quantified as open water pixels adjacent, or diagonal to, vegetation pixels. Edge was quantified with a 3×3 Laplacian edge detection filter (ERDAS, Imagine 11.0 2011). The presence/absence of a ditch or channel was recorded at bird survey points. Ditches were located either in front of, or directly adjacent to, the survey point, and ditches were defined as human-created, relatively deep, linear waterways. Ditches may influence wetland bird use of marsh, and this approach distinguished ditch use from the open water-vegetation edge effect. Overall, we analyzed marsh type (fresh or intermediate), management type (permanently impounded water, drawdown, unmanaged), and five fine-scale variables.

Analysis

Point counts had an unlimited radius, but only birds ≤100 m from a survey point were used for habitat analyses to minimize observer error and differences in detectability as well as to relate birds to fine-scale habitat. Species had high variability in their counts, so relative abundance was used whenever possible as an index of habitat use. Species were analyzed if they were detected at ≥10 % of points. Detection/nondetection was analyzed for species detected at <25 % of survey locations and for the gregarious dark ibis *Plegadis* spp. For species detected at ≥25 % of survey locations, mean relative abundance was used; large flocks of these species were not found. Detection/nondetection was interpreted as an index of habitat use. Since birds were wintering, migratory breeders, and resident breeders, relative abundance was measured as mean birds per point during the time frame of residence for each species. The mean of six surveys was used for resident birds (see Table 1 for species and residency status). For least bittern and purple gallinule, the last three survey visits were quantified. For yellowlegs and sora, the first three survey visits were used; American bittern and American coot detections were used from the first four surveys.

Generally, marsh birds were detected by auditory observations (e.g., king rail 96 % auditory), while shorebirds and wading birds were detected visually. For marsh birds, evidence shows detectability models are not improved by accounting for vegetation structure (see Darrah and Krementz 2009; Pickens and King 2012). The assumption of closure over the breeding season is also problematic for many birds (Rota et al. 2009), including king rail which can have two distinct home range areas (Pickens and King 2013). Wading birds and wintering species are also likely to violate the closure assumption. To be cautious, the solitary and difficult-to-observe green heron *Butorides virescens* and tricolored heron *Egretta tricolor* were discarded. One-sided *t* tests were used to investigate if the distance to other species was greater in fresh marsh or with permanently impounded water where open water was greater and vegetation density was lower (see "Results"). For significant results, the frequency histogram was examined, and problematic species were discarded.

We used generalized linear models in SAS 9.1 (SAS Institute, Cary, NC) to test the single-scale effects of marsh type, management, and fine-scale habitat (α=0.05). This step served to screen variables, particularly for fine-scale analyses. A binomial distribution with a logit link was used for detection/nondetection data, and a quasi-Poisson distribution with a log link was used for relative abundance. Site was not

Table 1 Resident breeding, migratory breeding, and wintering wetland birds observed ≤100 m of a survey point (n=304) in coastal marsh of southwest Louisiana and southeast Texas, USA. Only species initially analyzed are listed

Species	Status	Scientific name	Number observed	Proportion of points
Common gallinule	Resident	*Gallinula galeata*	867	0.60
King rail	Resident	*Rallus elegans*	620	0.57
Least bittern	Migratory	*Ixobrychus exilis*	391	0.49
Purple gallinule	Migratory	*Porphyrio martinicus*	708	0.48
Black-necked stilt	Resident	*Himantopus mexicanus*	930	0.34
Dark ibis	Resident	*Plegadis* spp.	1,347	0.28
Sora	Wintering	*Porzana carolina*	127	0.25
American coot	Wintering	*Fulica americana*	1,247	0.18
White ibis	Resident	*Eudocimus albus*	465	0.18
Great egret	Resident	*Ardea alba*	630	0.17
Yellowlegs spp.	Wintering	*Tringa* spp.	135	0.14
Pied-billed grebe	Resident	*Podilymbus podiceps*	69	0.12
American bittern	Wintering	*Botaurus lentiginosus*	64	0.12

used as a random effect, since there was replication of the fixed effects of marsh type and management types. To test marsh type and management, year was used as a covariate to account for annual differences. We tested for the interaction of marsh type and management. When management was a factor, contrasts compared unmanaged marsh with drawdown and permanently impounded water. Then drawdown and permanently impounded water were compared. Nonlinear relationships in fine-scale data were explored with general additive models (Yee and Mitchell 1991). Later, predictor variables were transformed with quadratic functions for generalized linear models. Fine-scale variables were screened with univariate tests, and then a multiple regression was performed with backwards selection. Year was a potential explanatory factor for fine-scale models.

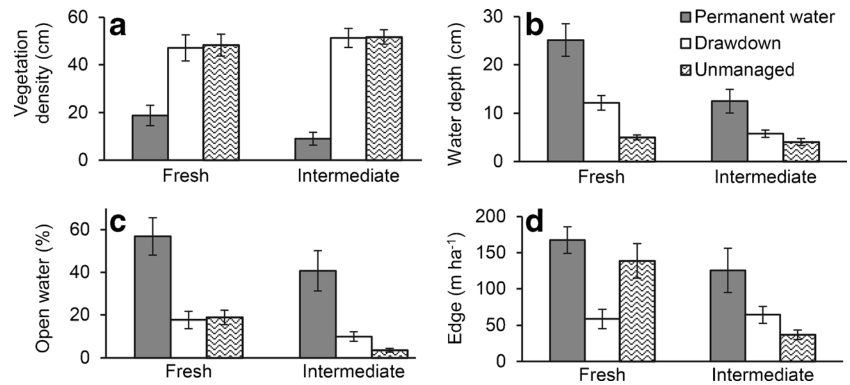
To compare habitat models of the three spatial scales and the combination of scales, we used Akaike's Information Criterion, corrected for small sample sizes, AIC_c (Burnham and Anderson 2002). The lowest AIC_c value represents the best model, and models within <2.0 of the best model are equally plausible, while models >4.0 are not well supported (Burnham and Anderson 2002). If year was retained in the fine-scale analysis, AIC_c results for marsh type and management were reported with year as a covariate; otherwise, year was not included in final analyses. To determine the explanatory power of Poisson models, we followed the approach of Thogmartin et al. (2006) by reporting the Spearman rank correlation between the observed and predicted abundance. For detection/nondetection models, the receiver operator characteristic's area under the curve (AUC) assessed the discrimination ability of models (e.g., Guisan and Zimmermann 2000; Aldridge and Boyce 2007). The AUC varies from 0 to 1.0, and it was interpreted as previously suggested: 0.50=no discriminatory power, 0.50–0.69=poor power, 0.70–0.89=good power, >0.90=excellent discriminatory power (Swets 1988; Manel et al. 2001). The receiver operator characteristic is useful because it is not dependent on animal prevalence or suitability thresholds. For species modeled with relative abundance, the AUC of a logistic model is reported for the same habitat variables, but with recalibrated parameter estimates. Means are reported ±1 SE.

Results

We surveyed 304 points over the 3-year study, and a total of 1,816 surveys were conducted. Thirty-two waterbird species were recorded, including 13 species with ample abundance to analyze (Table 1). Of these birds, marsh birds accounted for 4,093, wading birds 2,442, and shorebirds 1,065 of the total detected. Black-necked stilt were detected at a greater distance in fresh marsh (+11 m) compared to intermediate marsh, and great egret were detected at a greater distance in permanently impounded water (+13 m) compared to unmanaged/drawdown marsh. Therefore, both species were discarded from analyses. American bittern showed a marsh type difference (+20 m in fresh marsh), but the frequency histogram showed a similar peak in the recorded distance-to-bird. The result was likely caused by only ten American bittern being detected in intermediate marsh, so the species was retained for analysis. No other species had a significant t test.

Compared to intermediate marsh, fresh marsh was characterized by deeper water, more open water, and more edge (Fig. 2). Relative abundance of wetland birds differed greatly between fresh and intermediate marsh (Fig. 3). Wading birds and marsh bird swimmers (i.e., gallinules, American coot, pied-billed grebe) were more abundant in fresh marsh. Conversely, shallow water species, such as sora, king rail, least bittern, and yellowlegs, were more abundant in intermediate marsh. Relative bird abundance differed by management

Fig. 2 Summary statistics of fine-scale habitat variables by marsh type and management regime in northern Gulf Coast marshes. Water depth was measured late March–April; other variables were measured in late April. Means are reported ±1 SE



type with a primary pattern of wading birds and marsh bird swimmers being most common in marsh with permanently impounded water compared to other management types (Table 2; Online Resource 1). King rail and least bittern were the only birds positively associated with either drawdown or unmanaged areas (Table 2; Online Resource 1). The effect of management on king rail, purple gallinule, white ibis, and dark ibis depended on the interaction of marsh type and management (Table 2). Notably, king rail were most abundant with drawdowns in fresh marsh, but were most abundant in unmanaged intermediate marsh. A variety of fine-scale variables were correlated with bird abundance (Table 2; Fig. 4) with water depth being the most common. Species more abundant in fresh marsh usually had a positive, linear association with the water depths observed; least bittern and sora had a quadratic relationship while king rail had no relationship with depth (Fig. 4). In 2009, the spring following Hurricane Ike, dark ibis and white ibis were detected less than the other years. Common gallinule, king rail, and American coot were least abundant in the drought year of 2011, but yellowlegs were most common in 2011. The comparison of the three spatial scales consistently showed fine-scale habitat provided the best models compared to marsh type or management (Table 3). However, for 10 of 11 species' models, the combination of spatial scales was a better model than any single spatial scale ($\Delta AIC_c > 2.0$) (Table 3). The king rail was the only exception, as the models showed equal plausibility between the three scales combined and the interaction of marsh type and management. The Spearman correlation between the observed and predicted abundances explained a moderate amount of variance, and the AUC statistic rated all models as good at distinguishing detection and nondetection (AUC=0.76–0.84).

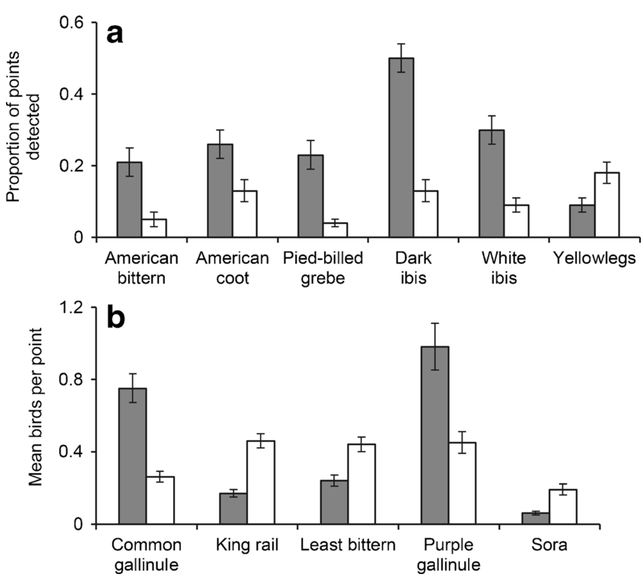


Fig. 3 Bird survey results from generalized linear models: **a** proportion of points with bird species detected and **b** mean birds per point from fresh marsh (n=130; *gray bars*) and intermediate marsh (n=174; *white bars*). Mean ±1 SE is reported. All species are significantly different by marsh type (α=0.05)

Discussion

Our hypothesis was supported because multiscale models of habitat selection were better than single-scale models for 10 of 11 coastal bird species. The results support the notion that fauna respond to multiple spatial scales of wetland flooding; these scales also represented varying temporal changes in habitat. Of the single-scale models, fine-scale habitat was frequently a better model than management or marsh type, but the results emphasize the importance of three distinctive, nonoverlapping scales. Other studies have shown habitat at multiple spatial scales affect wetland birds, such as land cover within varying radii (Pearse et al. 2012) or water depth combined with wetland area (Tozer et al. 2010; Webb et al. 2010). However, our study directly compared three distinct scales of factors related to hydrological characteristics in coastal marsh. Birds responded in a consistent manner to marsh type, management, and fine-scale habitat. This emphasizes the importance of water depth, and likely hydroperiod, to fauna at a variety of scales in coastal marsh.

The effect of marsh type has major implications because transitions are expected with climate change, levee systems (or lack thereof), river discharge or diversions, and sea-level rise (Costanza et al. 1990; Traill et al. 2011; Osland et al.

Table 2 The effect of management type and fine-scale habitat on mean relative abundance or detection/nondetection of birds in coastal marsh. Year was a covariate in all management models, and contrasts are reported with $\alpha=0.05$

Species	Management effect	Contrasts	Fine-scale variables
Common gallinule[a]	$F_{2, 299}=51.3$, $p<0.0001$	P>D>U	Depth (+), edge^2, open water^2, Vegdens (+), year
King rail[a]	$F_{2, 296}=10.14$, $p<0.001$[c]	Fresh=D>U, P/Int=U>D, P	Vegdens^2, year
Least bittern[a]	$F_{2, 299}=5.50$, $p=0.005$	U, D>P	Depth^2, ditch (+)
Purple gallinule[a]	$F_{2, 296}=5.04$, $p<0.01$[c]	Fresh=P>D, U/Int=D, P>U	Depth^2, ditch (+)
Sora[a]	$F_{2, 299}=1.60$, $p=0.20$		Depth^2
American bittern[b]	$F_{2, 299}=2.25$, $p=0.11$		Vegdens^2, year
American coot[b]	$F_{2, 299}=17.22$, $p<0.0001$	P>D, U	Vegdens (−), depth (+), edge^2, year
Dark ibis[b]	$F_{2, 296}=4.58$, $p<0.02$[c]	Fresh=P>D, U/Int=P, D>U	Vegdens (−), depth (+), edge^2, year
Pied-billed grebe[b]	$F_{2, 299}=11.84$, $p<0.0001$	P>D, U	Depth (+), edge (+), year
White ibis[b]	$F_{2, 296}=5.59$, $p<0.01$[c]	Fresh=no effect/Int=P>D, U	Vegdens (−), edge (+), year
Yellowlegs[b]	$F_{2, 299}=0.29$, $p=0.75$		Vegdens (−), depth (−), year

Quadratic relationships are shown as x^2

Int intermediate marsh, *P* permanently impounded water, *D* drawdown, *U* unmanaged

[a] Mean relative abundance

[b] Detection/nondetection

[c] Signifies the interaction of marsh type and management type

2013). Coastal bird studies have often concentrated on tidal salt marshes (e.g., Rush et al. 2009; Suazo et al. 2012), but threats of sea-level rise, storms, and salt water intrusion are likely to have substantial effects on nontidal, or wind-driven, systems. The differing bird abundances in fresh and intermediate marsh suggest direct, predictable effects of marsh type transitions on bird communities. For example, a conversion of fresh to intermediate marsh is predicted to decrease available habitat for gallinules, pied-billed grebes, and wading birds. Marsh vegetation zones are associated with a gradient of salinity and tidal influence (Crain et al. 2004; Snedden and Steyer 2012), but further research is needed to determine how water depth, hydroperiod, and water flow interact with salinity to dictate marsh types and their transitions. In addition, the effect of marsh types and management may be indicative of an "area effect" where an increased area of *suitable habitat* (e.g., deep water) increases abundance of certain bird species. Experimental evidence shows that conspecifics attract each other to habitats (Fletcher and Sieving 2010), and wetland birds may select habitat based on the presence of similar species (Ward et al. 2010).

Evidence regarding how water-level management affects wetland breeding birds has been lacking (Mitchell et al. 2006). Here, species that were more abundant in fresh marsh were positively associated with permanently impounded water. However, 2010 and 2011 were extremely dry, so unmanaged

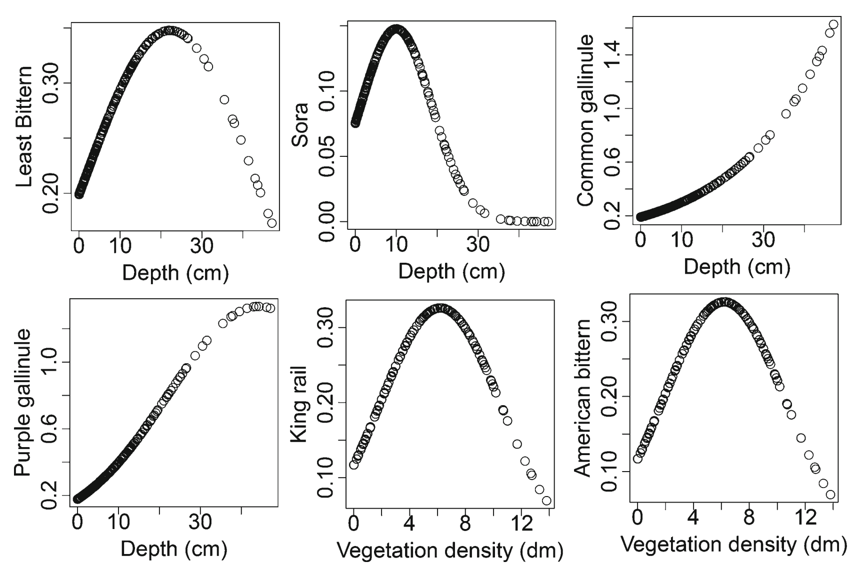


Fig. 4 A subset of univariate relationships of the fine-scale habitat features of water depth and vegetation density related to predicted relative bird abundance (least bittern, sora, common gallinule, purple gallinule, king rail) or probability of detection (American bittern). All variables were significant at $\alpha=0.05$

Table 3 Generalized linear models with the response of mean birds per point or detection/nondetection. All scales included the significant variables at the three spatial scales. The best models are in bold

Species	Scale	*K*	AIC_c	ΔAIC_c	Rho	AUC
Common gallinule[a]	**All scales**	**11**	**443.1**	**0.0**	**0.51**	**0.76**
	Fine scale	9	463.8	20.7		
	Management	4	481.5	38.4		
	Marsh type	4	502.3	59.2		
	Null+year	3	538.0	94.9		
Least bittern[a]	**All scales**	**7**	**390.3**	**0.0**	**0.52**	**0.77**
	Fine-scale	5	405.1	14.8		
	Marsh type	3	429.0	38.7		
	Management	3	429.4	39.1		
	Null	2	435.1	44.8		
King rail[a]	**All scales**	**8**	**377.6**	**0.0**	**0.58**	**0.85**
	Management[c]	**6**	**378.6**	**1.0**		
	Marsh type	4	393.2	15.6		
	Fine-scale	5	397.3	19.7		
	Null+year	3	412.3	34.7		
Purple gallinule[a]	**All scales**	**8**	**548.3**	**0.0**	**0.54**	**0.78**
	Fine scale	5	579.4	31.1		
	Management[c]	5	632.4	84.1		
	Marsh type	3	721.4	173.1		
	Null	2	749.6	201.3		
Sora[a]	**All scales**	**5**	**224.8**	**0.0**	**0.33**	**0.76**
	Marsh type	3	230.0	5.2		
	Fine scale	4	234.2	9.4		
	Management	NA				
	Null	2	238.2	13.4		
American coot[b]	**All scales**	7	**213.3**	**0.0**		**0.86**
	Fine scale	5	216.2	2.9		
	Management	4	252.0	38.7		
	Marsh type	4	279.0	65.7		
	Null+year	3	284.6	71.3		
Pied-billed grebe[b]	**All scales**	7	**169.3**	**0.0**		**0.86**
	Fine scale	5	173.9	4.6		
	Marsh type	4	204.9	35.6		
	Management	4	209.2	39.9		
	Null+year	3	287.2	40.7		
American bittern[b]	**All scales**	**6**	**169.0**	**0.0**		**0.82**
	Marsh type	4	179.4	10.4		
	Management	4	252.0	38.7		
	Marsh type	4	279.0	65.7		
	Null+year	3	191.3	22.3		
Dark ibis[b]	**All scales**	**10**	**229.4**	**0.0**		**0.91**
	Fine scale	7	242.9	13.5		
	Management[c]	6	267.5	38.1		
	Marsh type	4	302.0	72.6		
	Null+year	3	341.3	111.9		
White ibis[b]	**All scales**	**8**	**246.5**	**0.0**		**0.82**
	Management[c]	6	254.7	8.2		
	Fine scale	5	260.1	13.6		
	Marsh type	4	267.8	21.3		
	Null+year	3	228.2	58.9		
Yellowlegs[b]	**All scales**	**6**	**205.8**	**0.0**		**0.80**
	Fine scale	5	209.6	3.8		
	Management	NA				
	Marsh type	4	233.7	27.9		
	Null+year	3	238.2	32.4		

AUC area under the curve statistic, *Rho* Spearman correlation of the observed versus predicted abundance, *NA* variable not significant in univariate test

[a] Mean birds per point

[b] Detection/nondetection

[c] Interaction of management and marsh type

and drawdown marshes probably had abnormally low water levels. Species more abundant in the relatively shallow intermediate marsh (least bittern, sora, king rail, yellowlegs) were either negatively associated with permanently impounded water or had no association with management. Few studies have examined permanently impounded water or have simultaneously measured water depth and management. Nevertheless, the notion of management characterizing flooding depth and duration does show patterns. Shallow water species were studied by Gabrey et al. (2001), who showed two saltmarsh sparrows *Ammodramus* spp. and clapper rail were positively related to, or even restricted to, unimpounded marsh. Similarly, Fitzsimmons et al. (2012) showed the marsh bird group to be less abundant with spring drawdown management compared to unmanaged marsh in coastal Texas; conversely, wading birds and ducks were more abundant with drawdown management. While the effects of permanently impounded water and unmanaged marsh were consistent with water depths in our study, the effect of drawdowns was highly variable. For example, king rail abundance was greatest with drawdowns in fresh marsh, but greatest in unmanaged intermediate marsh. This habitat selection did not directly correspond to water depths (Fig. 2). Instead, the result is likely related to the drawdown date and, specifically, the availability of temporary ponds in late spring, which have been associated with the species via remote sensing (Pickens and King 2012). In intermediate marsh, the earlier drawdowns typically left few ponds into spring (April–June), and king rails were negatively affected. In fresh marsh, drawdowns were conducted later, and temporary ponds persisted later into spring.

Marsh birds have most commonly been associated with open water-vegetation edges (Weller and Spatcher 1965; Rehm and Baldassarre 2007; Rush et al. 2009). Of the eight marsh bird species in our study, three species were associated with edge, four with vegetation density, and six with water depth. Water depth is an important predictor for wading birds (Bancroft et al. 2002), shorebirds, and ducks (Colwell and Taft 2000), but our comprehensive results provide new evidence for its importance to marsh birds. Additionally, fine-scale measures assisted to explain broad-scale patterns. Birds with a positive, primarily linear relationship with water depth had increased abundance in fresh marsh and permanently impounded water, which had deeper water and likely a longer hydroperiod. In contrast, the quadratic relationship with water depth for sora and least bittern corresponded to their greater abundance in intermediate marsh; least bittern were also least abundant with the deep permanently impounded water. For American bittern and king rail, the quadratic relationship with vegetation density likely represented selection of both herbaceous vegetation structure and a few openings with open water. The presence of ditches was only associated with least bittern and purple gallinule. Given that other species were commonly observed in ditches (e.g., common gallinule, pied-billed grebe), we suggest ditch habitat use may be influenced by surrounding marsh conditions for other species.

Fine-scale habitat measures depicted interannual changes in weather and management decisions. For example, water depth explained least bittern and purple gallinule abundance, and year was not a factor. The repeated survey locations at JD Murphree in 2009 and 2010 were able to quantify annual variation within drawdown management areas. Both species were much more abundant in 2009 when water was held on the impoundments later in the season (due to Hurricane Ike and mitigation for saltwater intrusion), and this was characterized with positive associations with spring water depths. The earlier drawdown in March of 2010 resulted in dry spring conditions and few of these migratory birds. A few studies suggest that drawdown management regimes, as conducted in our study, may limit marsh bird abundance because deep winter water levels may limit emergent vegetation (Mitchell et al. 2006; Fitzsimmons et al. 2012). Our descriptive results showed little difference in spring vegetation density between drawdown and unmanaged areas (Fig. 2), although this does not account for winter conditions. Additionally, a concurrent radio telemetry study of king rail showed they selected for emergent marsh near open water and had larger home ranges in drier marsh, including drawdown areas at JD Murphree (Pickens and King 2013). Here, the survey results of six of eight species are consistent with the interannual effects of water depths described in least bittern populations (Jobin et al. 2009).

Management Implications and Conclusions

Our study quantified an unprecedented diversity and abundance of marsh birds in the northern Gulf Coast marshes and underscores the importance of the region for resident and migratory birds. The region is also under threat due to high rates of wetland loss (Stedman and Dahl 2008). By studying a large wetland region, we were able to quantify wetland bird–habitat relationships, which are otherwise difficult to obtain when wetland area is a dominant limiting factor. The findings indicate coastal wetland birds respond to multiple spatiotemporal scales of hydrological characteristics, and the consistency of the relationships highlight the importance of water depth, and potentially hydroperiod, at the scale of marsh type, management, and fine-scale habitat. Marsh type and management are factors to consider in regional conservation planning, localized management, or selecting appropriate indicator species. We caution that the short-term benefits of permanent water impoundments may have negative long-term effects on vegetation, such as *Typha* expansion (Boers and Zedler 2008), whereas short-term benefits of spring drawdowns may lead to excessive oxidation of organic soils under some circumstances. Furthermore, the timing of drawdowns and interannual variability in spring water levels can greatly affect migratory and breeding wetland bird abundance. Drawdowns of water before migratory bird arrival will result in fewer wetland birds unless the marsh is reflooded after annual germination.

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References

Aldridge, C.L., and M.S. Boyce. 2007. Linking occurrence and fitness to persistence: habitat-based approach for endangered greater sage-grouse. *Ecological Applications* 17: 508–526.

Bancroft, G.T., D.E. Gawlik, and K. Rutchey. 2002. Distribution of wading birds relative to vegetation and water depths in the northern Everglades of Florida, USA. *Waterbirds* 25: 265–277.

Boers, A., and J. Zedler. 2008. Stabilized water levels and *Typha* invasiveness. *Wetlands* 28: 676–685.

Bryant, J.C., and R.H. Chabreck. 1998. Effects of impoundment on vertical accretion of coastal marsh. *Estuaries and Coasts* 21: 416–422.

Burnham, K.P., and D.R. Anderson. 2002. *Model selection and multimodel inference: a practical information-theoretic approach.* New York: Springer Science+Business Media, Inc.

Colwell, M.A., and O.W. Taft. 2000. Waterbird communities in managed wetlands of varying water depth. *Waterbirds* 23: 45–55.

Conway, C.J. 2011. Standardized North American marsh bird monitoring protocol. *Waterbirds* 34: 319–346.

Conway, C.J., and J.P. Gibbs. 2011. Summary of intrinsic and extrinsic factors affecting detection probability of marsh birds. *Wetlands* 31: 403–411.

Conway, C.J., and C. Sulzman. 2007. Status and habitat use of the California black rail in the southwestern USA. *Wetlands* 27: 987–998.

Cooper, T.R. 2008. *King rail conservation plan and status assessment.* Fort Snelling, MN: U.S. Fish and Wildlife Service.

Costanza, R., S.C. Farber, and J. Maxwell. 1989. Valuation and management of wetland ecosystems. *Ecological Economics* 1: 335–361.

Costanza, R., F.H. Sklar, and M.L. White. 1990. Modeling coastal landscape dynamics. *Bioscience* 40: 91–107.

Cowan, J.H., R.E. Turner, and D.R. Cahoon. 1988. Marsh management plans in practice—do they work in coastal Louisiana, USA? *Environmental Management* 12: 37–53.

Crain, C.M., B.R. Silliman, S.L. Bertness, and M.D. Bertness. 2004. Physical and biotic drivers of plant distribution across estuarine salinity gradients. *Ecology* 85: 2539–2549.

Darrah, A.J., and D.G. Krementz. 2009. Distribution and habitat use of king rails in the Illinois and Upper Mississippi River Valleys. *Journal of Wildlife Management* 73: 1380–1386.

ERDAS. 2011. Imagine 11.0. ERDAS, Atlanta, Georgia, USA.

Fitzsimmons, O.N., B.M. Ballard, M.T. Merendino, G.A. Baldassarre, and K.M. Hartke. 2012. Implications of coastal wetland management to nonbreeding waterbirds in Texas. *Wetlands* 32: 1057–1066.

Fletcher, R.J., and K.E. Sieving. 2010. Social-information use in heterogeneous landscapes: a prospectus. *Condor* 112: 225–234.

Gabrey, S.W., A.D. Afton, and B.C. Wilson. 2001. Effects of structural marsh management and winter burning on plant and bird communities during summer in the Gulf Coast Chenier Plain. *Wildlife Society Bulletin* 218–231.

Greenwood, M.D. 2007. Nekton community change along estuarine salinity gradients: can salinity zones be defined? *Estuaries and Coasts* 30: 537–542.

Guisan, A., and N.E. Zimmermann. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* 135: 147–186.

Gunter, G., and W.E. Shell. 1958. A study of an estuarine area with water-level control in the Louisiana marsh. *Proceedings of the Louisiana Academy of Sciences* 21: 5–34.

Jobin, B., L. Robillard, and C. Latendresse. 2009. Response of a least bittern (*Ixobrychus exilis*) population to interannual water level fluctuations. *Waterbirds* 32: 73–80.

King, R.S., A.H. Hines, F.D. Craige, and S. Grap. 2005. Regional, watershed and local correlates of blue crab and bivalve abundances in subestuaries of Chesapeake Bay, USA. *Journal of Experimental Marine Biology and Ecology* 319: 101–116.

Lotze, H.K., H.S. Lenihan, B.J. Bourque, R.H. Bradbury, R.G. Cooke, M.C. Kay, S.M. Kidwell, M.X. Kirby, C.H. Peterson, and J.B.C. Jackson. 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* 312: 1806–1809.

Manel, S., H.C. Williams, and S.J. Ormerod. 2001. Evaluating presence-absence models in ecology: the need to account for prevalence. *Journal of Applied Ecology* 38: 921–931.

Meanley, B. 1969. *Natural history of the king rail. Account 67 in N. America fauna.* Washington DC: Bureau of Sport Fisheries and Wildlife.

Mitchell, L.R., S. Gabrey, P.P. Marra, and R.M. Erwin. 2006. Impacts of marsh management on coastal-marsh bird habitats. *Studies in Avian Biology* 32: 155.

Mitsch, W.J., and J.G. Gosselink. 2007. *Wetlands*, 4th ed. Hoboken, NJ: Wiley.

Montague, C.L., A.V. Zale, and H.F. Percival. 1987. Ecological effects of coastal marsh impoundments: a review. *Environmental Management* 11: 743–756.

Naugle, D.E., K.F. Higgins, S.M. Nusser, and W.C. Johnson. 1999. Scale-dependent habitat use in three species of prairie wetland birds. *Landscape Ecology* 14: 267–276.

Osland, M.J., N. Enwright, R.H. Day, and T.W. Doyle. 2013. Winter climate change and coastal wetland foundation species: salt marshes vs. mangrove forests in the southeastern United States. *Global Change Biology* 19: 1482–1494.

Pacheco, C., and P.K. McGregor. 2004. Conservation of the purple gallinule (*Porphyrio porphyrio* L.) in Portugal: causes of decline, recovery and expansion. *Biological Conservation* 119: 115–120.

Pearse, A.T., R.M. Kaminski, K.J. Reinecke, and S.J. Dinsmore. 2012. Local and landscape associations between wintering dabbling ducks and wetland complexes in Mississippi. *Wetlands* 32: 859–869.

Penland, S., and J.R. Suter. 1989. The geomorphology of the Mississippi River Chenier Plain. *Marine Geology* 90: 231–258.

Pickens, B.A. 2012. Modeling the spatial and temporal dynamics of coastal marsh birds. Ph.D. dissertation, Louisiana State University, Baton Rouge, LA.

Pickens, B.A., and S.L. King. 2012. Predicting the spatial distribution of king rails in an agricultural landscape. *Condor* 114: 113–122.

Pickens, B.A., and S.L. King. 2013. Microhabitat selection, demography, and correlates with home range size for the king rail (*Rallus elegans*). *Waterbirds* 36: 319–329.

Poulin, B., G. Lefebvre, S. Allard, and R. Mathevet. 2009. Reed harvest and summer drawdown enhance bittern habitat in the Camargue. *Biological Conservation* 142: 689–695.

Rehm, E.M., and G.A. Baldassarre. 2007. The influence of interspersion on marsh bird abundance in New York. *Wilson Journal of Ornithology* 119: 648–654.

Robel, R.J., J.N. Briggs, A.D. Dayton, and L.C. Hulbert. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. *Journal of Range Management* 23: 295–297.

Rogers, D., B. Rogers, and W. Herke. 1994. Structural marsh management effects on coastal fishes and crustaceans. *Environmental Management* 18: 351–369.

Rota, C.T., R.J. Fletcher Jr., R.M. Dorazio, and M.G. Betts. 2009. Occupancy estimation and the closure assumption. *Journal of Applied Ecology* 46: 1173–1181.

Rozas, L., and T. Minello. 2010. Nekton density patterns in tidal ponds and adjacent wetlands related to pond size and salinity. *Estuaries and Coasts* 33: 652–667.

Rush, S.A., E.C. Soehren, M.S. Woodrey, C.L. Graydon, and R.J. Cooper. 2009. Occupancy of select marsh birds within northern Gulf of Mexico tidal marsh: current estimates and projected change. *Wetlands* 29: 798–808.

Snedden, G.A., and G.D. Steyer. 2012. Predictive occurrence models for coastal wetland plant communities: delineating hydrologic response surfaces with multinomial logistic regression. *Estuarine, Coastal and Shelf Science* 118: 11–23.

Stedman, S., and T.E. Dahl. 2008. Status and trends of wetlands in the coastal watersheds of the eastern United States 1998 to 2004. National Oceanic and Atmospheric Administration, National Marine Fisheries Service and U.S. Department of the Interior, Fish and Wildlife Service: Washington DC.

Suazo, C.G., A.M. Arriagada, and J.R. Rau. 2012. Ephemeral aquatic bird assemblages in estuarine wetlands from south-central Chile: using an intertidal flat habitat during the austral summer. *Estuaries and Coasts* 35: 1137–1143.

Swets, J.A. 1988. Measuring the accuracy of diagnostic systems. *Science* 240: 1285–1293.

Thogmartin, W.E., M.G. Knutson, and J.R. Sauer. 2006. Predicting regional abundance of rare grassland birds with a hierarchical spatial count model. *Condor* 108: 25–46.

Tozer, D.C., E. Nol, and K.F. Abraham. 2010. Effects of local and landscape-scale habitat variables on abundance and reproductive success of wetland birds. *Wetlands Ecology and Management* 18: 679–693.

Traill, L.W., K. Perhans, C.E. Lovelock, A. Prohaska, S. McFallan, J.R. Rhodes, and K.A. Wilson. 2011. Managing for change: wetland transitions under sea-level rise and outcomes for threatened species. *Diversity and Distributions* 17: 1225–1233.

Visser, J.M., C.E. Sasser, R.G. Linscombe, and R.H. Chabreck. 2000. Marsh vegetation types of the Chenier Plain, Louisiana, USA. *Estuaries* 23: 318–327.

Ward, M.P., T.J. Benson, B. Semel, and J.R. Herkert. 2010. The use of social cues in habitat selection by wetland birds. *Condor* 112: 245–251.

Webb, E.B., L.M. Smith, M.P. Vrtiska, and T.G. Lagrange. 2010. Effects of local and landscape variables on wetland bird habitat use during migration through the Rainwater Basin. *The Journal of Wildlife Management* 74: 109–119.

Weller, M.W., and C.S. Spatcher. 1965. Role of habitat in the distribution and abundance of marsh birds. Agricultural and Home Experiment Station Special Report 43, Iowa State University: Ames, Iowa.

Wiens, J.A. 1989. Spatial scaling in ecology. *Functional Ecology* 3: 385–397.

Yee, T.W., and N.D. Mitchell. 1991. Generalized additive models in plant ecology. *Journal of Vegetation Science* 2: 587–602.

Multi-Scale Habitat Selection of Wetland Birds in the Northern Gulf Coast
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Supplemental Material: Online Resource 1

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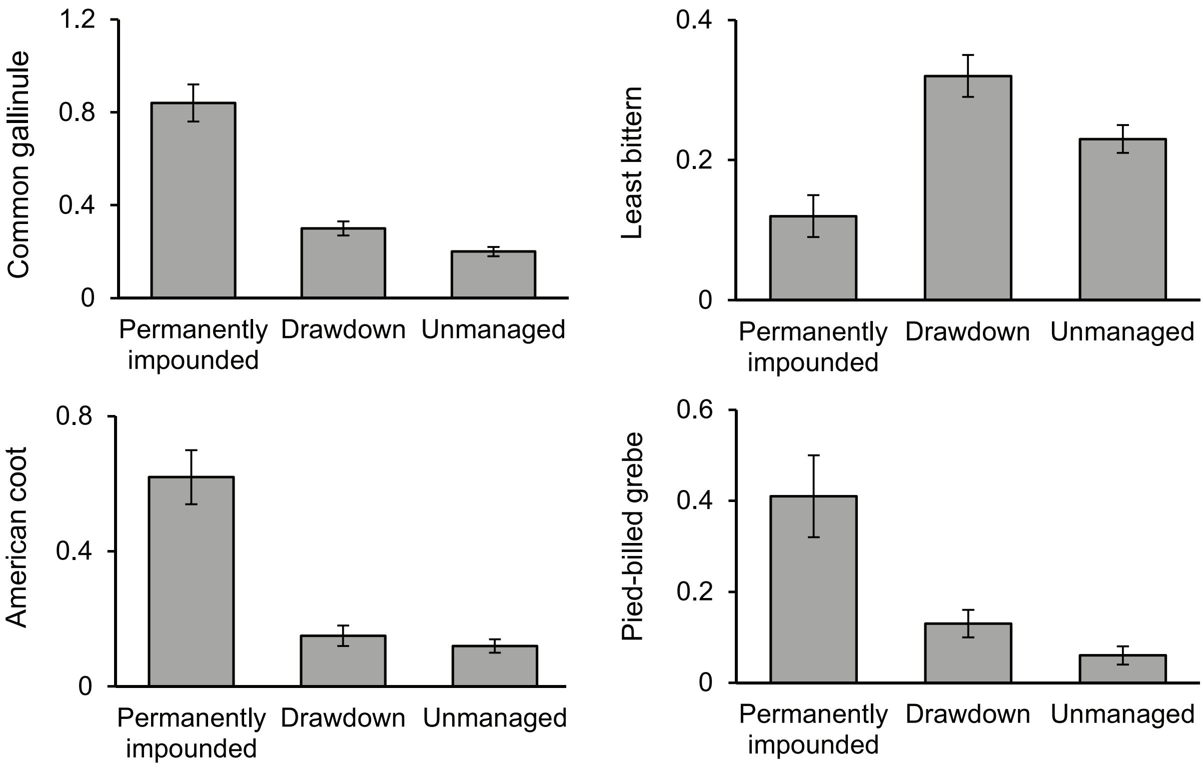

Fig. S1 The univariate effect of management type on wetland bird mean abundance (common gallinule, least bittern) and detection/nondetection (American coot, pied-billed grebe) in coastal Louisiana and Texas, USA. Error bars are ± 1 SE

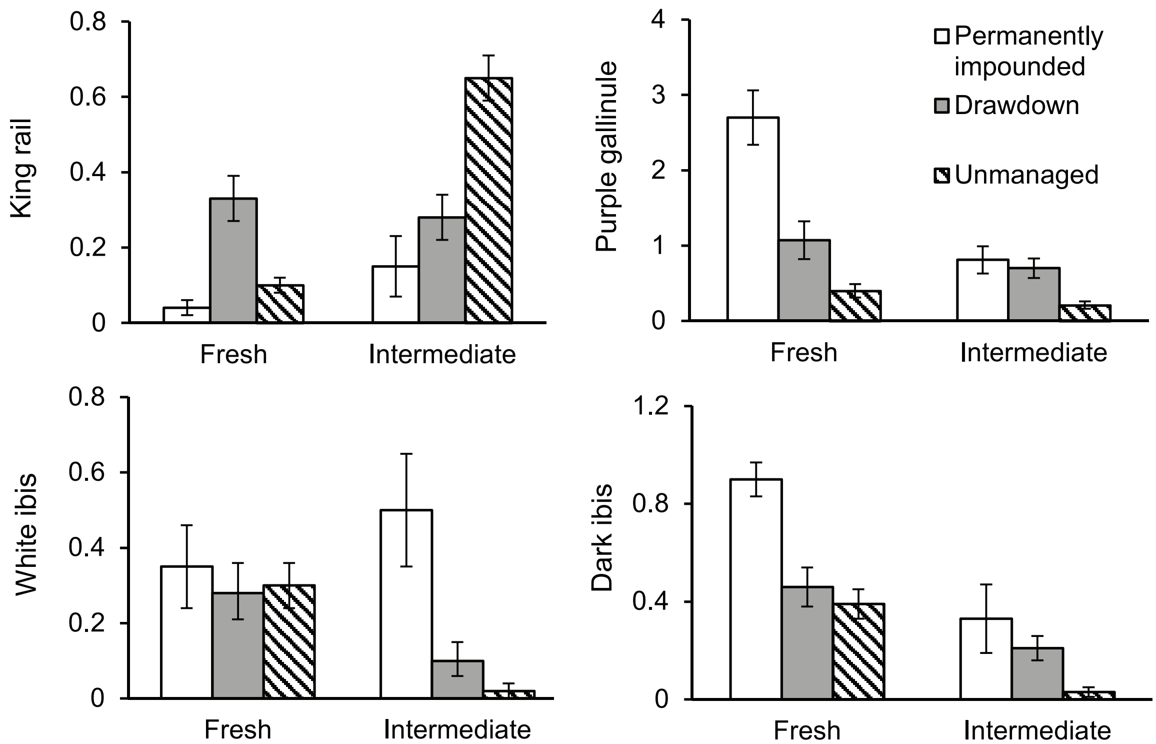

Fig. S2 The interaction effect of management type and marsh type on wetland bird abundance (king rail, purple gallinule) and detection/nondetection (white ibis, dark ibis) in fresh and intermediate marshes of Louisiana and Texas, USA. Error bars are ± 1 SE