

MODELING THE SPATIAL AND TEMPORAL DYNAMICS OF
COASTAL MARSH BIRDS

A Dissertation

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DEDICATION

My dissertation is dedicated to my wife, Christine Pickens. I could not have accomplished this without your help, kind words of encouragement, plus all of your jokes and bell-jumps. To my parents, Walt and Lorali Pickens, who provided everlasting support.

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ABSTRACT

Wetland birds are likely to be influenced by habitat at multiple spatial scales, yet few studies have investigated bird responses at both broad and fine scales. Northern Gulf Coast marshes are dynamic ecosystems, and they provide an ideal place to examine habitat across spatial and temporal scales. My research focused on the secretive marsh bird guild (i.e. bitterns, rails, gallinules, grebes) with an emphasis on the king rail (*Rallus elegans*), a species of high conservation concern. My objectives were to investigate the wetland bird-environment relationship across scales, and to model annual changes in bird distribution. Study sites were in the fresh and intermediate (oligohaline) marshes of the Chenier Plain coastal region of southwest Louisiana and southeast Texas. I captured king rails for a two year radio telemetry study, and conducted point count surveys of marsh birds from March to mid-June of 2009-2011 using call-back methods to elicit responses. I visited each point six times per year, and >100 points were surveyed each year ($n=304$). Localized, field-based measures (e.g. water depth), management, and broad marsh types were related to bird abundance, and species distribution models were developed for four species based on Landsat satellite imagery. Home ranges of king rails varied from 0.8-32.8 ha ($n=22$), rails selected for open water, and smaller home ranges were associated with greater open water within the home range (20-30%). Point counts showed fine-scale habitat models, usually incorporating water depth, were improved with the addition of broad-scale marsh type and management, classified as permanently impounded, drawdown, or unmanaged. For 11 of 12 species, a multi-scale model was better than any single spatial scale. Species distribution models showed satellite-based measures of habitat corresponded well to marsh birds as they explained 37-79% of the variation in abundance. Temporary water was the most important variable, and species' models were distinct for fresh and intermediate marshes. The

spatial distribution of birds varied greatly among years, especially with migratory birds in the highly variable fresh marsh. Overall, marsh birds responded to the environment at a variety of spatial scales, and satellite-based distribution models showed broad-scale patterns and dynamic distributions among years.

CHAPTER 1: INTRODUCTION

Landscape ecology has been developing since 1950 when Carl Troll first coined the term by linking the concept of geography with the ecosystem (Troll 1950). In wildlife ecology, Johnson (1980) has recognized a hierarchy of four distinct spatial scales of habitat selection: geographic range, home range selection, within home range selection, and the selection of sites for specific activities, such as foraging. These spatial scales and their intrinsic link to geography are the basis for many of the multi-scale studies now common in ecology. There have been two distinct paths taken by ecologists and wildlife biologists. At a very coarse spatial scale, experts in biogeography have discovered that climate-based models of species distribution are improved with land cover data (Luoto et al. 2007, Tingley and Herman 2009). Meanwhile, wildlife ecologists have often focused on local-scale phenomenon, such as vegetation structure, and in the past few decades, they have discovered the broader landscape often drives species' distributions (e.g. Mitchell et al. 2001). In my dissertation, I wish to bridge this gap and build a framework that develops a better integration of wildlife ecology and geography.

Coastal wetlands have a history of being a prime subject of landscape ecology due to its many changes over space and time (see Costanza et al. 1990). Marshes are dynamic ecosystems with temporal changes due to rainfall, drought-wildfire relationships, and anthropogenic factors (Han et al. 2007). Meanwhile, spatial heterogeneity is driven by the interactions of flooding, fires, herbivory, people, topography, management, and weather events, such as wind-driven tides or hurricanes. Eastern coastal wetlands currently comprise 38% of the total wetlands in the contiguous United States, and the Gulf of Mexico coast has experienced the highest wetland loss rate (Stedman and Dahl 2008). Much of this loss is in freshwater wetlands (Stedman and Dahl

2008). Yet, the wildlife of coastal wetlands has received little attention despite being a popular subject among ornithologists and tourists alike.

Large-scale restoration efforts in Gulf Coast marshes are primarily based on plants, but animals represent a broader suite of wetland functions. Kwak and Zedler (1997) examined the trophic structure of invertebrates, fish, and marsh birds in salt marsh; they concluded the clapper rail (*Rallus longirostris*) was the top predator. Indeed, wetland birds have been used as ecological indicators of wetland functions because of their strong link to mercury or contaminant exposure (Zhang et al. 2006, Cumbee et al. 2008), hydrological regime (Desgranges et al. 2006, Frederick et al. 2009), and prey species (Frederick et al. 2009). Therefore, a better understanding of the ecology of wetland birds and their link to coastal processes would be beneficial.

Furthermore, monitoring animal populations is inherently difficult and efficient techniques are needed to monitor broad-scale areas, measure changes in abundance over time, and predict the consequences of coastal change. Species distribution modeling using advanced technologies, such as satellite remote sensing and geographic information systems (GIS), has the potential to link local wetland functions to broad-scale monitoring of animal populations.

In my study, I examined wetland birds in fresh and intermediate (oligohaline) marsh types in southwestern Louisiana and southeast Texas (see Visser et al. 2000 for a description). The fresh marshes are dominated by *Typha* sp., *Panicum hemitomon*, and *Sagittaria lancifolia*, while intermediate marshes are dominated by *Spartina patens*, *Phragmites australis*, *Schoenoplectus* sp., *Typha* sp., and *Paspalum vaginatu*. Intermediate marshes are sometimes classified with brackish marsh, but I classify the marshes here as intermediate because it fits the description of oligohaline marshes and not the mesohaline wiregrass classification as described by Visser et al. (2000). My study area is part of the Chenier Plain, which encompasses many

natural ridges that restrict tidal flow (Penland and Suter 1989) (Figure 1.1). Along with the relatively small tides of the northern Gulf Coast, much of the marsh flooding is due to seasonal wind-driven tides (Penland and Suter 1989) and rainfall. Additionally, my study area encompassed a longitudinal gradient that rapidly decreases in mean annual precipitation as one proceeds to the southwest. (see Woo and Winter 1993 in Mitsch and Gosselink 2007).

In my study, I was particularly interested in the habitat use of secretive marsh birds (i.e. rails, bitterns, gallinules, grebes) because many of these birds have apparently declined throughout the United States over the last 30 years and are listed as species of conservation concern (Conway 2011). Few of these species are easily quantified in standardized surveys, such as the USGS Breeding Bird Survey (Conway 2011), so the status of populations is poorly known. In particular, the king rail (*Rallus elegans*) is a high conservation priority because of its threatened or endangered status in 12 eastern and Midwestern U.S. states and Canada (Cooper 2008). Similar to other marsh birds, information on king rail densities, habitat associations, movements, spatial distribution, and demographic rates are largely unknown. The northern Gulf Coast marshes are thought to be a stronghold for the king rail (Cooper 2008), and research in this region has the opportunity to inform management actions throughout the species' range.

At a localized spatial scale, the guild of secretive marsh birds are associated with vegetation structure, open water, water depth, and open water-vegetation edge (Lor and Malecki 2006, Rehm and Baldassarre 2007, Jobin et al. 2009). Vegetation composition has also been related to birds (Conway et al. 1993, Conway and Sulzman 2007), but few other habitat variables have been explored. For example, topographic heterogeneity and gradual dewatering have been suggested to provide rail habitat (Eddleman et al. 1988), but the effects have not yet been tested. Given the ecological importance of flooding in wetlands (Mitsch and Gosselink 2007), and

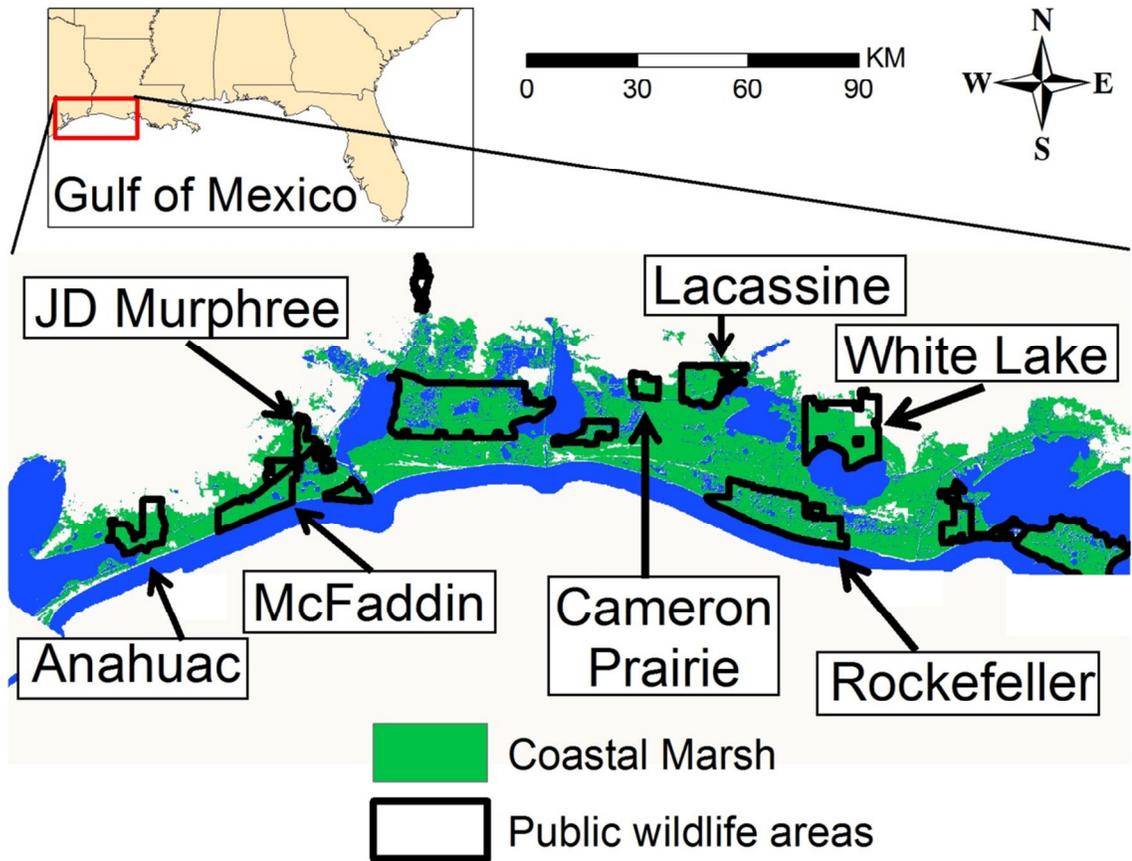


Figure 1.1 Study sites in southwestern Louisiana and southeastern Texas, USA. White Lake, Lacassine, and the majority of Cameron Prairie were fresh marsh. Intermediate marshes included Anahuac, JD Murphree, McFaddin, and Rockefeller

the broad-scale nature of flooding regimes, broad spatial scales are likely to influence the spatial distribution of wetland birds. Broad-scale factors range from the distribution of managed impoundments to precipitation patterns and elevation within the region. Likewise, the temporal dynamics of coastal wetlands is likely to affect the demography and the spatial distribution of birds on the marsh landscape.

My study was affected by two major events that altered the environment considerably. Hurricane Ike (Sept. 12, 2008) and Hurricane Gustav (Sept. 1, 2008) severely impacted the coast of Louisiana and Texas before my first study year in the spring of 2009. Hurricane Ike created

storm surges >5 meters at McFaddin National Wildlife Refuge, and saline conditions were still present at Texas study sites throughout the 2009 spring season. Secondly, a severe drought in 2011 (-45 cm from normal January-May precipitation) strongly influenced marsh ecology, including marsh birds, open water, water depth, and the seasonality of flooding conditions. These highly variable habitat conditions provided an opportunity to learn more about how the distribution of coastal marsh birds varies over time.

OBJECTIVES AND ORGANIZATION OF CHAPTERS

The planning and design of my dissertation research focused on the king rail because of its high conservation priority status in the region. However, the understanding of a single species is enhanced by providing context of other similar species in the same environment. Therefore, I provide a thorough analysis of several wetland bird species. The overarching objectives of my dissertation were: 1) quantify how habitat features relate to the abundance, distribution, and movement of wetland birds in a coastal environment; 2) examine the species-environment relationship over multiple spatial scales and determine how the relationship changes with spatial scale; 3) use satellite remote sensing for developing species distribution models to predict relative bird abundance and to examine broad spatial patterns of bird distribution in the coastal region; 4) quantify how these spatial patterns change over time and within fresh and intermediate marsh types. In this regard, my dissertation is organized into three research chapters, each of which investigates new spatial and temporal scales from a different perspective. As the dissertation progresses, inferences from the previous chapter are used to ask more broad questions about species, coastal wetlands, and ecological interactions over space and time.

Chapter 2 is a fine-scale study focused on king rail movements, home range, and microhabitat selection. I ask questions related to habitat selection within the home range of the

king rail and how this selection may affect the rail's movements to meet its requirements for food and shelter. In Chapter 3, I examined a suite of wetland birds (wading birds, shorebirds, secretive marsh birds) by linking bird point counts with habitat measured at the spatial scale of marsh type (fresh or intermediate), management areas, and local factors measured within 100 m of bird survey points. I focused Chapter 4 on four secretive marsh bird species, and I used satellite remote sensing to link the distribution of these birds to spatial habitat components and habitat over time.

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CHAPTER 2: MICROHABITAT SELECTION, DEMOGRAPHY, AND INFLUENCES ON HOME RANGE SIZE FOR THE KING RAIL

INTRODUCTION

Understanding species movements and home ranges can provide insights into species-environment interactions (Lorenz et al. 2011), the influence of food resources (Santangeli et al. 2012), and the area of habitat required for species (Powell et al. 2010). Comparatively large home ranges have been associated with higher energetic demand (McNab 1963, Harestad and Bunnell 1979), and recent studies have shown animals with smaller home ranges are often associated with better fitness. For example, crows and ravens (*Corvus* sp.) had higher survivorship and smaller home ranges near human settlements (Marzluff and Neatherlin 2006) and mallards (*Anas platyrhynchos*) with smaller home ranges were more likely to have successful nesting attempts (Mack and Clark 2006). Since abundance obtained from typical counts is not always an indicator of high quality habitat (e.g. Pidgeon et al. 2006), a behavioral approach can lead to a better understanding of how particular habitats meet the needs of species (Pickens and Root 2009). Furthermore, the understanding of microhabitat selection, defined here as habitat selection within the home range (see Johnson 1980 for an overview), can identify what resources are being selected, and the abundance of such resources (e.g. foraging areas). Microhabitat selection is a useful fine-scale measurement because other studies have demonstrated home range estimates alone were not enough to determine fine-scale habitat features (e.g. Powell et al. 2010).

The king rail (*Rallus elegans*) is a marsh bird of high conservation concern for the United States, including the southeastern region (Hunter et al. 2006). The king rail has been listed as a threatened or endangered species in the 12 eastern and midwestern states as well as Canada; apparent declines have been severe in these regions (Cooper 2008). Other species of secretive

marsh birds (e.g., gallinules, grebes, bittern, rails) have shown habitat associations with open water, water depth, and open water-vegetation edge (Lor and Malecki 2006, Rehm and Baldassarre 2007), but little is known about the king rail. King rails tend to avoid woody vegetation in interior wetlands (Darrah and Krementz 2009, Pickens and King 2012), but information is lacking on their density, demography, habitat selection, home range, and movements. Answers to these questions would assist in estimating population sizes, identifying factors driving population dynamics, and understanding habitat requirements. In general, correlates with home range size have not been investigated for marsh birds, but the least bittern (*Ixobrychus exilis*) has shown dramatic variation in inter-annual home range size (mean= 91 ha vs. 564 ha), and an explanation for the variation is unclear (Griffin et al. 2009).

In this study, I used radio telemetry to investigate king rail habitat use in the coastal marshes of Louisiana and Texas during 2010 and 2011. Coastal marshes included fresh and intermediate (oligohaline) marsh types and 2011 was a severe drought year (-45 cm from normal January-May precipitation). I quantified king rail home range size and movements with the following objectives: 1) determine microhabitat selection of king rails in relation to water characteristics and vegetation composition; 2) correlate habitat characteristics with home range size; 3) quantify adult survivorship and compare chick/juvenile abundance over two years. I hypothesized king rails would have comparatively larger home ranges and greater movements when there was less open water habitat available.

METHODS

Study Area

The three study sites were located in the Chenier Plain coastal region of southwestern Louisiana and southeastern Texas. The Cheniers, or oak ridges, have a geologic history resulting from sediment deposition and the reworking of sediments from the Mississippi River Delta (Penland and Suter 1989), and the result is numerous natural ridges that prevent substantial tidal flow. Water levels are primarily determined by rainfall and seasonal wind-driven tides. I captured and monitored king rails in Texas at McFaddin National Wildlife Refuge (McFaddin), in 2010-2011 (94° 5' N, 29° 41' W), JD Murphree Wildlife Management Area (JD Murphree) in 2010 (94° 1' N, 29° 51' W), and in Louisiana, Cameron Prairie National Wildlife Refuge (Cameron Prairie) in 2011 (93° 3' N, 29° 57' W). McFaddin and JD Murphree were intermediate, or oligohaline, marshes dominated by *Spartina patens*, *Phragmites australis*, *Schoenoplectus* sp., *Typha* sp., and *Paspalum vaginatu* (see Visser et al. 2000). Cameron Prairie had both fresh and intermediate marsh communities. Dominant vegetation at Cameron Prairie included *Typha* sp., *Schoenoplectus californicus*, *S. patens*, and *P. australis*.

Capture and Radio Attachment

I captured king rails at McFaddin in 2010 and 2011, and this was the primary study site. To explore variability among sites, I also captured rails at JD Murphree, TX in 2010 and Cameron Prairie, LA in 2011. Trapping was conducted from March 11 to April 25, 2010 and March 9 to May 6, 2011. The first capture method was the use of an airboat at night to spotlight king rails and capture them with a dip net as described by Perkins et al. (2010). With this method, one driver and two catchers/spotlighters were used to flush rails and capture them. Airboats were used to capture rails in 2010, but the method was used sparingly in 2011 due to

dry marsh conditions. Second, I used drift line fences with drop-door traps (see Conway et al. 1993, Perkins et al. 2010). Drop-door Havahart traps were 24.1 x 24.1 cm x 87 cm with a 2.5 cm hard mesh frame, and plastic drift line fences with a height of 61 cm lead to the drop-door traps. Drift fencing was either placed in a V-shape or two traps were placed in back-to-back V-shapes to trap rails that moved behind the traps. Similar to audio lures used to catch sora rails (*Porzana carolina*) (Haramis and Kearns 2007), I used call-back recordings placed on or near the traps to facilitate rail movements into traps. Recordings were played continuously on a portable speaker attached to an MP3 player, and the calls consisted of three king rail calls from Stokes field guide to birds: eastern edition (1995) (30 sec each) and 30 seconds of silence.

After bird capture, I measured body mass (± 2.0 g), wing (± 1.0 mm), tail (± 0.1 mm), tarsus (± 0.1 mm), and exposed culmen (± 0.1 mm). Then a USGS aluminum band was fitted to the lower leg. I used a modified “glue-on” transmitter (Advanced Telemetry Systems, Isanti, MN; Model A2480, 40 ppm, 3.6 g) and attached the transmitter via a backpack harness similar to Dwyer (1972). The backpack harness was attached with 0.5 cm Teflon ribbon (Bally Ribbon Mills, Bally, PA), and the two loops encircling the wings were linked below the furcula with 1-2 cm of ribbon. Total weight of the package ranged from 7-8 g, and I only attached transmitters to birds when transmitter weight was $\leq 3\%$ body mass. The average handling time of captured birds was 35 minutes, and ranged from approximately 20 minutes to 1 hour.

King rails with estimated home ranges were sexed using morphological measurements with the discriminant function analysis presented by Perkins et al. (2009). They found 100% sex discrimination of king rails using this method, and also distinguished male king rails from salt marsh inhabiting clapper rails (*Rallus longirostris*). King and clapper rails 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 my study sites. Twelve of the 22 birds I used for home range analysis were readily identified as male king rails and were clearly much larger than either sex of clapper rail. Two birds were not clearly male or female by the morphology method, so I initially tested the effect of sex on home range size and movements with 20 of the 22 birds. Twelve of the analyzed king rails were male, eight were female, and two could not be identified.

Radio Telemetry and Microhabitat Selection

King rail locations were recorded starting forty-eight hours after capture to allow birds to become habituated to their transmitters. Birds were located from 2-6 days/week, but usually 3-4 days/week. Locations were primarily recorded within four hours of sunrise or sunset. All locations were separated by >7 hours with the goal of obtaining ≥ 30 locations per bird during the breeding season from March 9 to July 20. I used two methods to locate birds. Triangulation was performed with observers obtaining 3-5 bearings, and Locate 3.33 software (Nams 2010) was used to determine bird locations and location error. I used a global positioning system (GPS) with <6 m error to record Universal Transverse Mercator (UTM) coordinates. Two receiver types were used: portable receiver/antennae (model- TRX-16S, Wildlife Materials, Inc., IL, USA) and a box receiver (ATS, model- R2100) with a 3-element folding Yagi antennae. All azimuths were recorded within 20 minutes to minimize errors due to bird movements. I also used a homing, or "walk-in" method, as generally outlined by White and Garrot (1990) and previously used for black rail habitat selection (Tsao et al. 2009). Walk-ins were performed 1-2 times per week for each bird throughout the breeding season. Specifically, walk-ins were performed by informally triangulating a rail until the GPS location could be recorded with a distance and direction to the bird; king rails could often be approached within 10-15 m. When birds were observed to be nesting, I only performed one microhabitat measurement until nesting ceased or the bird moved

away from the location. Microhabitat selection was quantified from the walk-ins and several variables were recorded. Distance to open water was recorded with a maximum of 100 m due to visual constraints. Within a 10-m radius (0.03 ha) of the bird location, I recorded the percent cover of vegetation species, percent open water, and maximum water depth within emergent vegetation. Plant species percent cover was recorded for all species with $\geq 5\%$ cover within the 10-m radius. For maximum water depth of emergent marsh, three water depths were recorded for each vegetation species, and the maximum depth was used. To compare king rail microhabitat use versus availability within the home range, I randomly selected an azimuth and paced 50 m from each bird location in the random direction. The same habitat variables were measured for the random location. This immediate pairing of habitat use and habitat availability was useful for capturing current conditions, such as water depth, and minimized observer bias.

I quantified movements and estimated home ranges for birds with ≥ 30 locations, as a minimum of 30 locations has been deemed suitable for home range analysis (Seaman et al. 1999). King rail home ranges typically did not increase after 20-25 locations, but one bird at JD Murphree continued moving to new areas after a period of intense rainfall due to a tropical storm in July. Therefore, this bird at JD Murphree may have a conservative home range estimate. I calculated daily movements from consecutive locations spanning from 7 to 36 hours between locations. Triangulation locations were estimated using a fixed standard deviation error rate estimated annually from the dataset and applying the maximum likelihood estimation method. I eliminated all locations with 95% confidence ellipses > 1 ha. Bearing error estimates were 5.7° for 2010 and 10.0° for 2011.

Following the definition of the home range by Burt (1943), I quantified the breeding season home range for king rails between March 9 and July 20th. Territorial behavior was

variable, but commenced in early to mid-March, and by July 20th, all juveniles observed had complete juvenile plumage and were beginning to fly (see Meanley and Meanley 1958). I calculated the 50% core area and 95% kernel home range using Home Range Tools 1.1 in ArcGIS (Rodgers et al. 2007). I used a fixed-kernel estimation method, which uses a bivariate normal distribution (Worton 1989). The smoothing parameter was estimated via a least-squares cross-validation procedure. For the triangulation locations, the error classes were the following (ha): 0-0.2 = 55%; 0.2-0.4=27%, 0.4-0.6=10%, 0.6-0.8= 5%, 0.8-1.0=2%. Two birds had home ranges surrounding a large, deep bayou, so I eliminated the bayou from the home range estimate, since it was clearly unused. A total of seven observers performed telemetry in the two years of study and one observer was active in both years. Walk-ins consisted of 35% of the total locations recorded. To quantify error rates associated with walk-ins, transmitters were hidden in areas with similar vegetation to where birds were commonly found ($n=4$ per observer). Each observer followed the standard walk-in procedure and the error was recorded as distance from the transmitter.

Adult Survival and Reproduction

Thirty king rails were used in adult survivorship estimation; I monitored 14 birds in 2010 and 16 in 2011 for a total of 2,287 exposure days. Due to the lack of visuals on many radio tagged birds, I periodically ensured king rails were alive by eliciting responses with call-backs of king rail calls with a portable speaker, or ensured rails moved after a walk-in was completed. Mortalities within fourteen days of capture were not included in the survival analysis due to the possibility of stress and unusual behavior due to capture and transmitter attachment. I recovered dead birds as soon as possible, but the lack of a mortality signal on the radio transmitters meant some birds were not recovered in time to identify the predator. Predators were determined by

examination of bird remains. Carcasses with tooth marks on the feathers and transmitter were assumed to be eaten by a mammal, whereas feathers that were cleanly plucked were assumed to be predated by a raptor. Likely predators in the region include mink (*Mustela vison*), red fox (*Vulpes vulpes*), red-tailed hawk (*Buteo jamaicensis*), northern harrier (*Circus cyaneus*), American alligator (*Alligator mississippiensis*), and several snake species.

The presence of king rail chicks and juveniles at McFaddin were recorded for any birds observed during the course of study. Based on pictures associated with Meanley and Meanley (1958), chicks and juveniles were aged into the following biweekly categories: 1-2, 3-4, 5-6, 7-8, and >9 weeks. Since rails were observed opportunistically while radio telemetry was being conducted at McFaddin, I estimated observer search effort by totaling the number of bird locations in each year. This is likely to correspond with the hours that observers spent in the field, and a similar number of king rails were monitored with radio telemetry in both years. Due to the lack of chick or juvenile observations in 2011, I expended an extra two evenings in late June specifically searching for king rail chicks and juveniles.

Analysis

I analyzed microhabitat selection for birds with ≥ 5 walk-ins, and examined individual vegetation species if the plant was recorded at >10% of the total vegetation surveys. I included a category of "annual" plants that was dominated by *Amaranthus australis*, but also included Indian tobacco (*Rumex crispus*), *Sesbania* sp., sprangletop (*Leptochloa fascicularis*), and millet (*Echinochloa* sp.). This increased the sample size of these plants, and I expected king rails to respond similarly to annual wetland plants that require dry conditions to germinate. I quantified total emergent plant species richness, including wetland shrubs and trees. Plant species richness included *Distichlis spicata*, *Iva frutescens*, *Paspalum vaginatum*, *Phragmites australis*,

Schoenoplectus californicus, *Schoenoplectus robustus*, *Typha* sp., and *Spartina patens*. Floating plants were rare and were excluded from the analysis. Multi-collinearity ($r > 0.70$) was not a problem for any variables. I modeled microhabitat selection using a generalized linear model (SAS: Proc GLIMMIX) with a binomial distribution and a logit link. Individual birds were modeled as a random effect to account for the repeated measurements on each bird. I did not include a site effect for microhabitat selection since individual birds were already treated as a random effect, and therefore, habitat use was only compared with available habitat for each individual bird. I fit a global model with vegetation composition, distance to open water, percent open water, and maximum depth as variables. I used a backward selection process to obtain the final model ($\alpha = 0.05$) with year as a random effect.

I calculated mean daily movement and maximum distance between two locations for each bird. To test the independence of locations within the 7-36 hour time frame between locations, I performed a simple linear regression of the time interval between locations and distance the bird moved. For home range and maximum movement comparisons, I only tested birds at McFaddin for sex and year differences because home ranges differed substantially by site and only a few birds were monitored at JD Murphree and Cameron Prairie. Likewise, I tested for correlates of home range size (95% and 50% kernel density) and maximum movements within McFaddin ($n = 18$). For environmental variables, I combined the bird use and random surveys into a single mean value for each bird to characterize the home range. For example, mean open water for the home range was estimated from the bird walk-ins and their associated random locations. I only used percent open water, and not distance to open water, since it better depicted the overall habitat. I also tested for the effect of vegetation species that were selected by king rails. The method assumed that random locations within 50 m of a bird were within the bird's home range.

To analyze the effect of year, sex, and habitat components, I used a generalized linear model with a Gaussian distribution for the 95% kernel home range and a Poisson distribution with a log link for the 50% kernel home range and maximum movement analysis.

I calculated daily survivorship, then monthly survivorship, and cumulative breeding season survivorship for 2010 and 2011 (March 9- July 20) (see Kane et al. 2007 for details). I used all sites in the analysis to maximize my sample size. Telemetry was conducted until July 20 in 2010, but monitoring ended July 2 in 2011, so I only estimated survivorship in 2011 to July 2nd. I used a Kaplan and Meier (1958) survivorship curve estimator with a staggered entry design (Pollock et al. 1989). I right censored birds that were still alive at the end of the study period, or with the last known location for birds that disappeared due to transmitter failure, large movements, or unknown fates. The analysis assumed no negative transmitter effects, the fate of right censored individuals was random and independent of survivorship, and left censored birds had a survivorship distribution similar to previously monitored birds (Pollock et al. 1989). Birds were entered into the survival analysis 24 hours after capture. I used the R package 'asbiol' for survival analysis and all other analysis was conducted with SAS 9.1 (SAS Institute, Cary, NC). Means are reported ± 1 SE unless otherwise noted.

RESULTS

I captured 17 king rails in 2010 and an additional 17 in 2011. When the backpack harness was initially being modified in 2010, I had three birds lose transmitters within 48 hours of attachment. These birds were deleted from all analyses. Of the remaining birds, four were monitored at Cameron Prairie in 2011, three at JD Murphree in 2010, and 24 at McFaddin for both years combined. For the walk-in analysis, I performed a total of 239 walk-in surveys on 24 birds (median=11 surveys per bird), and the median observer error rate for locating transmitters

was 4 m ($n=40$). Compared to the nearby random points, the results of microhabitat selection showed king rails selected for a higher percent cover of *Typha* ($F_{1,441}=6.35$, $p=0.01$), *Schoenoplectus robustus* ($F_{1,441}=6.15$, $p=0.01$), and *Phragmites australis* ($F_{1,441}=14.95$, $p=0.0001$) (Figure 2.1). Plant species richness ($F_{1,441}=9.94$, $p=0.002$) was higher in areas used by king rails, although the effect size of plant species richness was relatively small (2.48 ± 0.07 vs. 2.18 ± 0.07). All other plant species were used in proportion to their availability. Distance to open water was negatively associated with king rail microhabitat use ($F_{1,441}=13.11$, $p=0.0003$), as rails were closer to water compared to the nearby random points ($15.4\text{m} \pm 1.5$ vs. $21.5\text{m} \pm 1.6$). Percent open water and maximum water depth did not differ between used and random locations.

For home range analysis, I recorded a total of 1079 locations from 30 birds, and I estimated home ranges and movements for 22 rails. For these 22 birds, the median number of locations per bird was 43. There was no relationship with the time between location estimates and movement distance within a 36 hour time frame ($F_{1,656}=0.05$, $p=0.82$), which underscores the independence of locations with intervals of >7 hours. Home range size varied greatly among sites, and the four largest home ranges were for the birds at JD Murphree and Cameron Prairie (Table 2.1). Three of these four birds made a large movement and set up a second home range (e.g. Figure 2.2). The other bird at JD Murphree did not set up a second home range, but did make a brief movement of over 2 km and continued to extend its range after a tropical storm provided intense rainfall and marsh flooding. On occasions where king rail captures were near each other, the overlap of home ranges was minimal (Figure 2.2). The maximum movement between two locations was 2578 m.

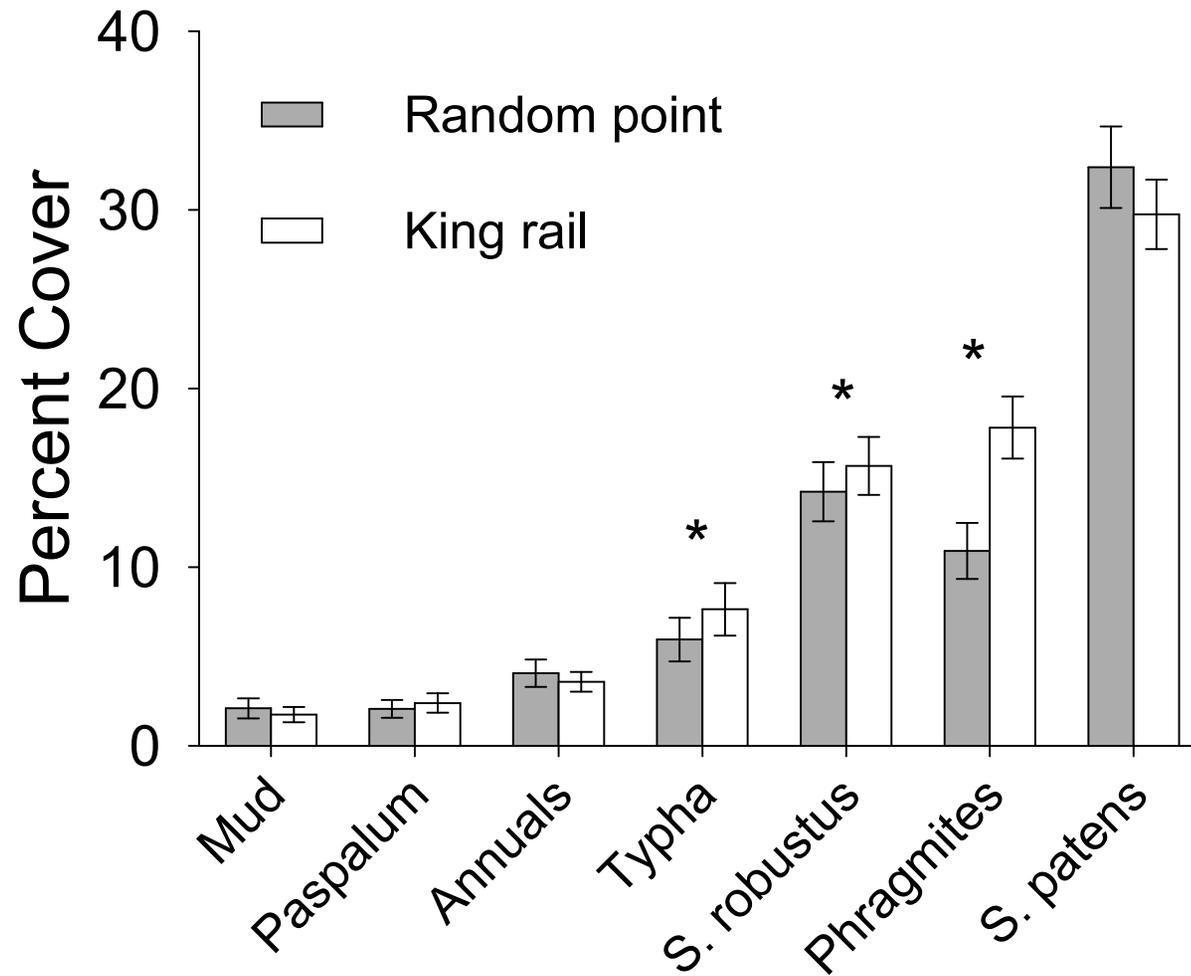


Figure 1.1. Vegetation composition of locations used by king rail versus random locations 50 m from birds. As indicated by asterisk (*), *Typha* sp., *Schoenoplectus robustus*, and *Phragmites australis* were used more by king rails compared to random.

At McFaddin, king rail maximum movement, 95% and 50% kernel density home range size did not differ by sex or year. I found open water was negatively related to the 95% kernel density home range size ($F_{1,16}=4.74$, $p=0.04$, $r^2=0.23$) (Figure 2.3). Smaller home ranges were associated with more open water, and the smallest home ranges had 20-30% open water. There was a trend towards smaller core areas (50% kernel) ($F_{1,16}=4.03$, $p=0.06$) and shorter maximum movements ($F_{1,16}=4.24$, $p=0.056$) (Figure 2.4), but these relationships were not significant at the $\alpha=0.05$ level. No vegetation species were associated with home range size or maximum movements.

I estimated daily survivorship (\pm SE) as 0.999 ± 0.001 in 2010 and 0.995 ± 0.002 in 2011. The cumulative survivorship probability was 90% for the breeding season in 2010 and 60% in 2011 (Figure 2.5). In 2010, only one adult king rail mortality was observed, and the predator was suspected to be a watersnake (*Nerodia* sp.) because of the time it spent in ditches, but the cottonmouth (*Agkistrodon piscivorus*) is also a possibility. The transmitter was tracked under cement pilings, holes along a bank, and within ditches. Mortalities in 2011 were categorized as one avian, one mammal, and three unknown. Censored birds included two transmitter failures and one bird found underneath a power line.

At McFaddin, I observed 139 king rail chicks and juveniles in 2010, and a variety of age classes were observed (Figure 2.6). For comparison purposes, 110 of the 139 were observed by June 30, 2010. For the same breeding period ending June 30, 2011, I observed a total of 16 king rail chicks at McFaddin. In 2010, the mean (\pm 1SD) of chicks per family group was 4.7 ± 2.6 chicks/group for the 1-2 week age class, 2.9 ± 1.7 chicks/group for 3-4 week age class, and 1.9 ± 1.0 rails/group for age classes greater than 5-6 weeks. The maximum number of

Table 2.1. Home range kernel density estimates and movement characteristics of the king rail (*Rallus elegans*) in Louisiana and Texas coastal marshes for 2010-2011. Mean \pm 1SE are given, and the range of the 95% kernel home range is given in brackets.

Site	95% home range (ha)	50% home range (ha)	Maximum distance between 2 locations (m)	Daily movements (m)
McFaddin (<i>n</i> =18)	4.4 \pm 0.6 [0.8-10.4]	0.89 \pm 0.12	359 \pm 33	78.4 \pm 4.9
JD Murphree (<i>n</i> =2)	27.3 \pm 5.5 [21.8-32.8]	4.99 \pm 0.62	1955 \pm 624	257.6 \pm 69.6
Cameron Prairie (<i>n</i> =2)	11.9 \pm 4.1 [7.7-16.0]	2.66 \pm 0.98	1409 \pm 361	143.9 \pm 40.5

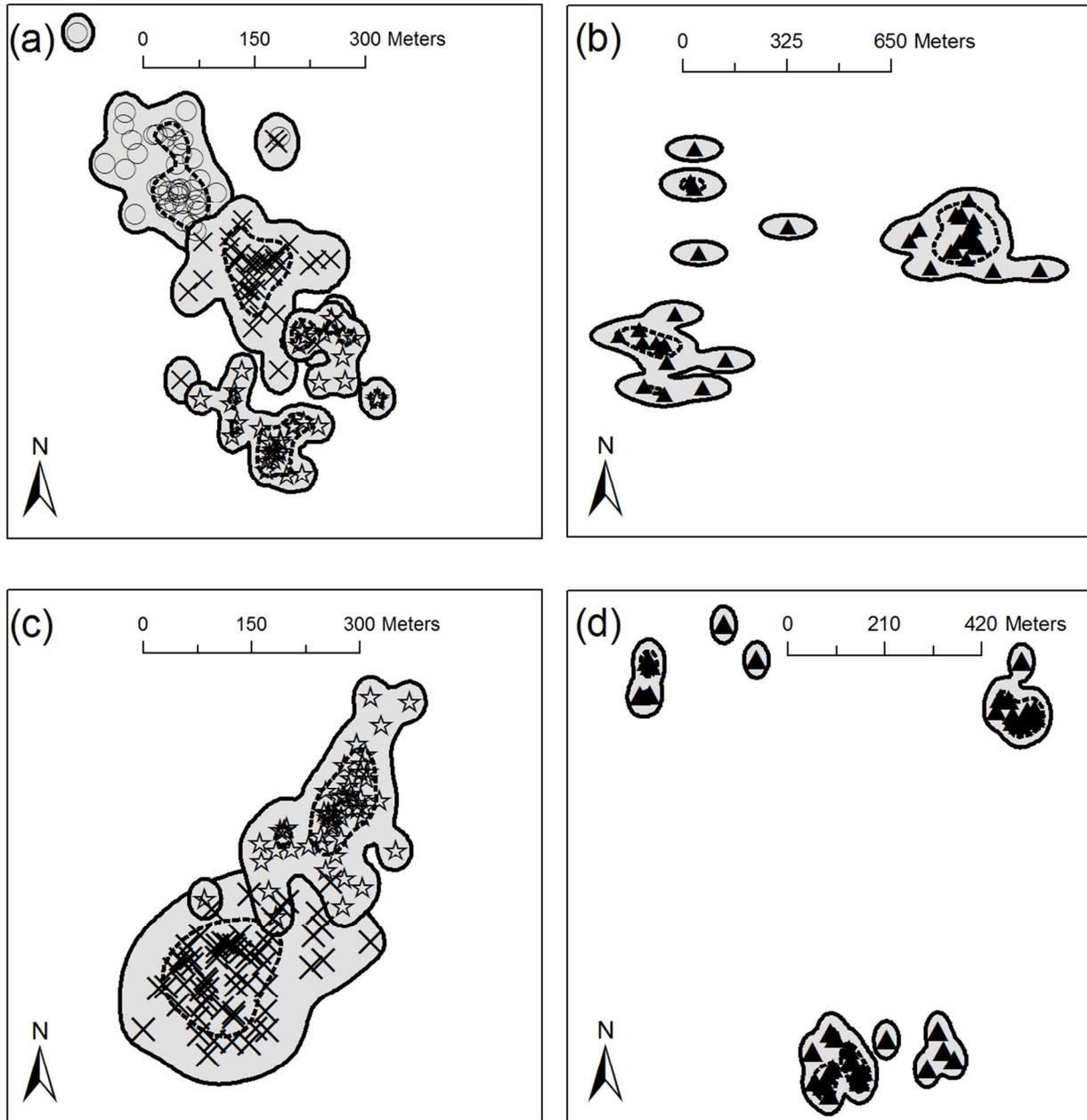


Figure 2.2. Examples of king rail (*Rallus elegans*) home ranges as depicted by dark lines representing the 95% kernel density home range and dashed lines representing the 50% kernel density home range. Locations of individuals are marked with circles, x's, and stars. (a) 3 individuals at McFaddin, (b) 1 individual at JD Murphree, (c) 2 individuals at McFaddin, (d) 1 individual at Cameron Prairie.

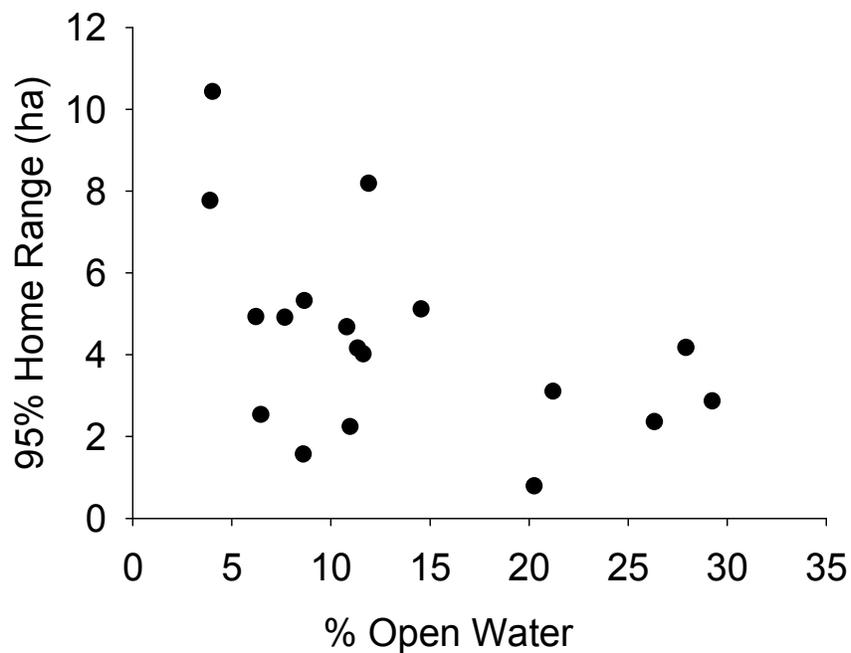


Figure 2.3. The relationship between percent open water within king rail (*Rallus elegans*) home ranges and their 95% kernel density home range estimated for 18 king rails at McFaddin National Wildlife Refuge, TX.

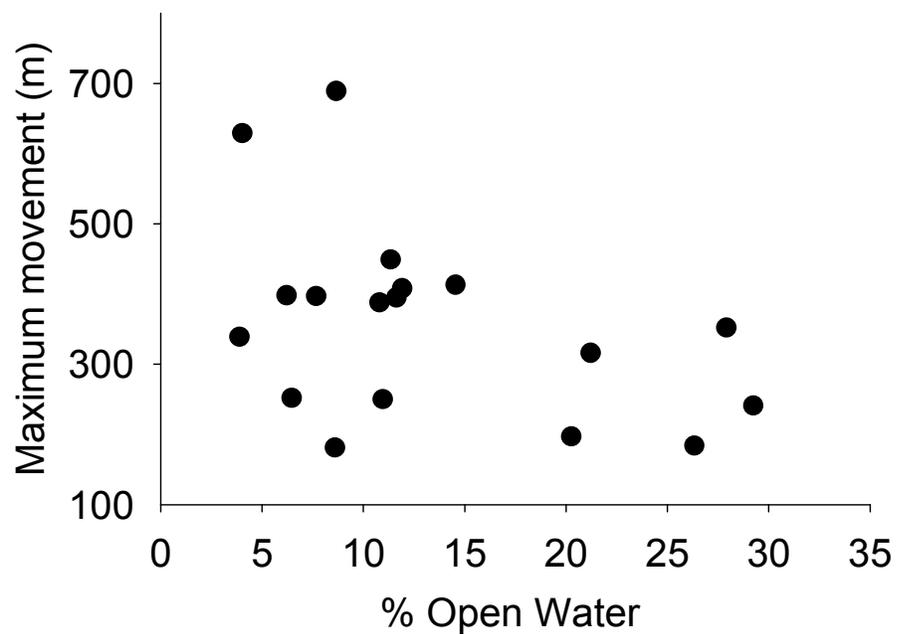


Figure 2.4. The relationship between percent open water within king rail (*Rallus elegans*) home ranges and their maximum distance between two locations at McFaddin National Wildlife Refuge, TX.

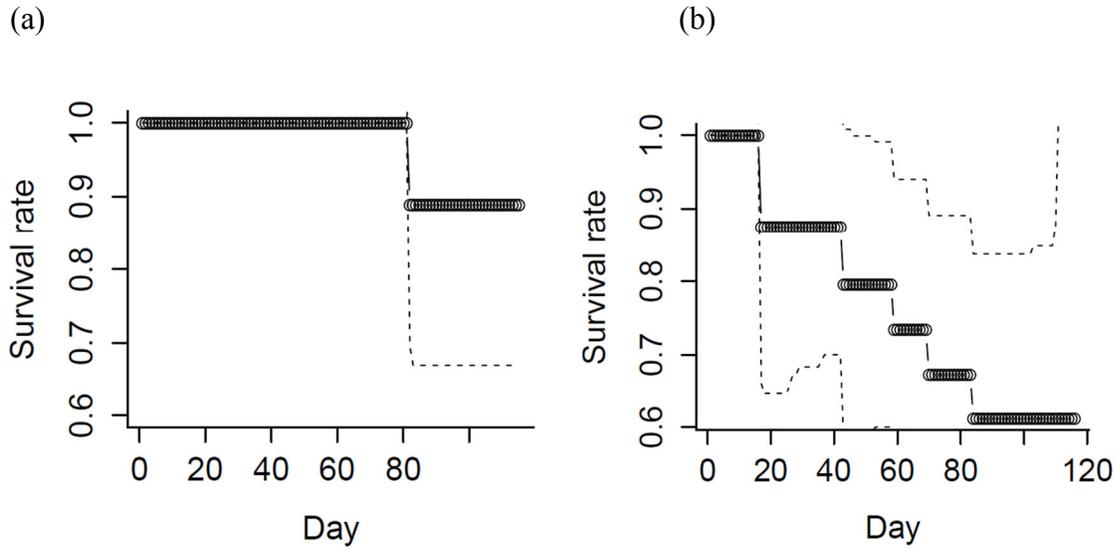


Figure 2.5. Kaplan-Meier survivorship curve for the king rail (*Rallus elegans*) for (a) 2010 and (b) the drought year of 2011. Dashed lines represent the 95% confidence intervals.

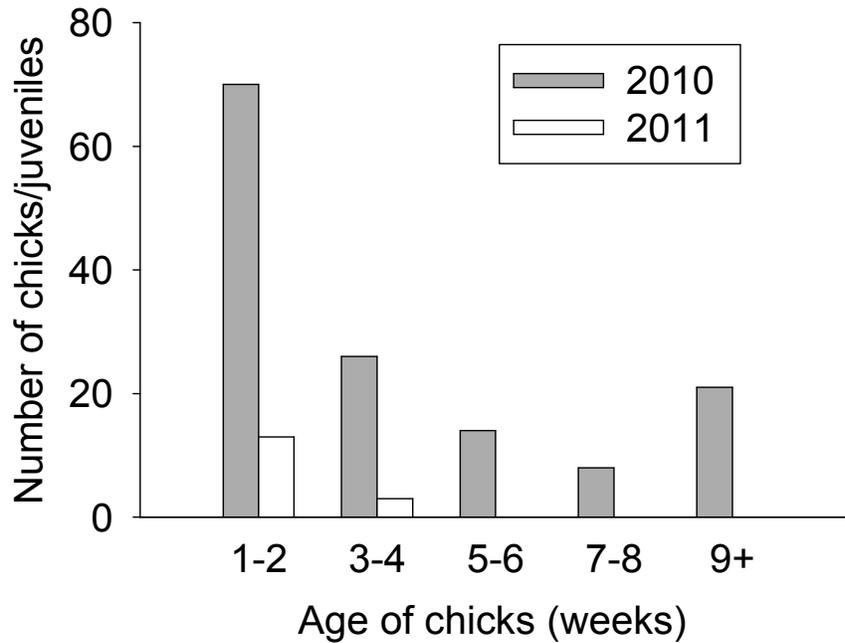


Figure 2.6. The number of king rail (*Rallus elegans*) chicks and juveniles observed at McFaddin National Wildlife Refuge, TX in 2010 and the drought year of 2011.

chicks/group was eight. As a measure of search effort for the period ending June 30th of both years, I estimated 447 bird locations in 2010 and 424 locations in 2011. No chicks or juveniles were observed beyond the 3-4 week age class during the drought year of 2011 despite the similar search effort.

DISCUSSION

I found king rails selected microhabitat based on distance to open water, plant species richness, and plant species that are generally associated with open water, comparatively wet areas, and dense cover. The home ranges and movements of king rails had large variability between sites. The range of 95% kernel density home ranges was between 0.78 and 32.8 ha. I hypothesized that birds with less available open water would have larger home ranges, and the results supported this idea. Additionally, the correlation with home range size may explain why large site differences existed. Although limited in sample size, my demographic results revealed a substantial negative effect of drought on the reproduction and survival of king rails.

Typically, avian field studies measure habitat within 100 m of a bird survey location, and then compare relative abundance with points separated by over 250 m (see Chapter 3 & 4). This method fundamentally measures selection at the spatial scale of an animal's home range (see Johnson 1980). Here, I demonstrate that king rails select habitat features within their home range. During microhabitat surveys, I found king rails were closer to open water compared to random points merely 50 m from the bird. Rails were often found near small ponds, along bayous, along a permanent lake, and ditches. Interestingly, water depth was not being selected by birds at this spatial scale, although many water depth measurements were zero during the course of my study. A wetter year may have yielded different results, but another possibility is the birds are responding to either long-term flooding or water depth at a spatial scale beyond the

microhabitat scale I tested. King rails used patches of *Phragmites* extensively during my study, but I emphasize that *Phragmites* is not invasive in the northern Gulf Coast region and most patches were small (<50m²). In the early winter, *Phragmites* provided structure and cover while other species, such as *Typha*, were senesced. Plus, *Phragmites* usually occupied a slight topographic gradient, which provided for heterogeneous water levels. *Typha* was selected by king rails, and in the oligohaline marsh type, *Typha* usually occupied a narrow fringe around small ponds where king rails were present. Monocultures of *Typha* were rarely used, and king rails at Cameron Prairie even appeared to fly over large stands of *Typha* before reaching open water areas. The heterogeneity, or patchiness, of vegetation selected by king rails was also demonstrated by the selection of marsh with a greater plant species richness compared to nearby points. The vegetation diversity association observed with this microhabitat study could also be reflected by the correlation of king rails with the heterogeneity of wetness in my remote sensing analysis (see Chapter 4).

King rails had extremely variable home range sizes by site. At McFaddin, where a high density of birds made trapping more feasible, home ranges were consistently smaller than the other sites. Indeed, both Cameron Prairie and JD Murphree had much less suitable habitat according to my species distribution models (Chapter 4). The two birds at Cameron Prairie had large movements from the original trapping location, and as the marsh dried, both rails moved to their second home range area for the rest of the season. All three king rails with two distinct seasonal home ranges moved to more flooded locations as the first home range area dried. Interestingly, all of these birds moved back to their first home range area for a few days after occasional rain events. Afterwards, the rails moved to their second home range area again. For least bittern, fifteen percent of birds used two distinct territories during the breeding season in

New York, but birds moved less than 500 m to do so (Bogner and Baldassarre 2002). In comparison to king rail home ranges observed here (0.8-32.8 ha), clapper rails (*Rallus longirostris*) inhabiting tidal salt marshes had much smaller breeding season home ranges with a mean of 1.4 ha (95% kernel density) (Rush et al. 2010) or smaller (Zembal et al. 1989). However, the fresh marsh Yuma clapper rail (*Rallus longirostris yumanensis*) used a similar home range area of 7-8 ha with mean daily movement distances of 126-157 m (Conway et al. 1993). The home range size requirements among species may reflect the consistency of available resources (i.e. tidal vs. non-tidal), but the density of animals can also restrict home range sizes (Benson et al. 2006). In my study, I found home range sizes within McFaddin were correlated with available open water within the home range. When open water was more common, birds had smaller home ranges. As indicated by the maximum movements between locations, king rails also tended to venture away from their core home range when conditions were dry. Overall, these results support the notion that the home range size of wetland birds may be a good surrogate for habitat quality when other information is unavailable.

Adult survivorship data are sparse for Rallidae. In my study, king rail adult survivorship for the breeding season was relatively high in 2010 (90%), but low during the 2011 drought (60%). Conway et al. (1994) estimated survival for 36 Virginia rail (*Rallus limicola*) and 20 sora (*Porzana carolina*) with a mean exposure period of 47 days per bird. In their study, no mortality was observed in the breeding season, but non-breeding cumulative survivorship was low for sora 0.308 ± 0.003 and Virginia rails 0.54 ± 0.191 . Wetland birds have shown susceptibility to drought conditions in the past, with yellow-headed blackbirds (*Xanthocephalus xanthocephalus*) being reduced in density and lacking any reproduction due to predators (Fletcher and Koford 2004). Nest success for secretive marsh birds is commonly reported as being >50% (Lor and Malecki

2006, Pierluissi and King 2008), but little information exists for chick and juvenile survival, especially for the precocial Rallidae. The drought of 2011 had a dramatic impact on king rail reproduction with no juveniles being observed. In 2010, predation appeared to limit juvenile numbers, since the mean group size went from 4.7 for chicks in the 1-2 week age class to 1.9 for ages above 5-6 weeks. While these observations were opportunistic, to my knowledge, this is the first reporting of king rail chick and juvenile numbers, and I have demonstrated the effect of drought on Rallidae survivorship and reproduction.

In summary, king rails selected microhabitat within 50 m of their location, and rails selected habitat closer to open water with a patchy mosaic of vegetation species. Survivorship and reproduction declined dramatically in the year of drought. Importantly, king rails with more open water within their home range had smaller home range sizes, and the smallest home ranges were found with 20-30% open water. Therefore, management should consider providing open water habitat within this range with the objective of increasing the density of king rails. Further research is needed with other wetland birds to identify correlates of home range size and to establish whether home range size may be indicative of habitat quality or density of birds.

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CHAPTER 3: A MULTI-SCALE ASSESSMENT OF WETLAND BIRD HABITAT USE

INTRODUCTION

Coastal wetlands in the eastern United States comprise 38% (16.1 million ha) of the total wetlands of the conterminous United States (Stedman and Dahl 2008), and the high amount of primary productivity of these marshes is well established (Teal 1962, Hopkinson et al. 1978, Darby and Turner 2008). The upper trophic levels of fish, shrimp, crabs, shellfish, ducks, and a diverse assemblage of resident and migratory birds give coastal wetlands an extremely high socio-economic value. Yet, wetland loss is a major problem in coastal regions due to human modifications of the hydrological regime; mechanisms such as subsidence, lack of accretion or sedimentation, canal-building for oil and gas extraction or navigation, increases in urbanization, and salinity intrusion all contribute to losses in varying degrees (Turner 1997, Day et al. 2000, Pauchard et al. 2006). The Gulf of Mexico coast currently has the highest coastal wetland loss in the United States with over 200,000 ha lost between 1998 and 2004 alone (Stedman and Dahl 2008). While much research has focused on coastal marsh plants, the fundamental habitat use of birds, and the spatial scales upon which birds are affected, are poorly known. A thorough understanding of coastal bird habitat use will assist with evaluating species vulnerability to coastal wetland loss and to manage available habitat in an optimal condition.

The influence of spatial scale on animal distribution and habitat use is prominent in ecology (Wiens 1989), but there is a basic lack of knowledge about the spatial scale of the species-environment relationship for wetland birds (Bancroft et al. 2002). The dominant influence on wetlands, the flooding regime, is operational at a broad scale because of rainfall, broad elevation classes, and salinity; the result is generally represented as dominant vegetation types, or a particular suite of plant species in a region. A medium scale of influence is due to

water-level management with structures such as levees and pumps, while fine-scale attributes include the effect of microtopography, and the resulting localized variation in water and vegetation structure.

The spatial scale of wetland bird habitat selection studies has differed based on the bird assemblage under consideration and data availability, but few studies have simultaneously compared multiple scales. Wading bird studies have used aerial flight surveys and broad-scale hydrological data (Bancroft et al. 2002, Russell et al. 2002) or fine-scale effects of vegetation, water depth, and prey items (Lantz et al. 2010, Pierce and Gawlik 2010). Meanwhile, shorebird habitat use has been primarily measured at moderate scales (e.g. Taft and Haig 2006), such as habitat within 10-km, but fine-scale data is rarely compared. Research on secretive marsh birds (i.e. rails, bitterns, gallinules, grebes) has concentrated on associations between birds or nests and localized habitat, such as open water or vegetation composition (Conway et al. 1993, Lor and Malecki 2006, Conway and Sulzman 2007). From all of these wetland bird studies, there are few, if any, occasions when spatial scales are combined or fine-scale scales are compared to more broad scales.

Here, I examined the habitat use of wetland birds at three distinct spatial scales relevant to management and monitoring of marsh birds. At the broadest scale, fresh and intermediate (oligohaline) marsh types represent a dominant suite of plant species, which are likely to be dependent on a general hydroperiod and salinity tolerance. Marsh types encompass tens of thousands of hectares in coastal Louisiana and Texas. At a medium spatial scale, I assessed water-level management, which determines the depth, duration, and seasonality of flooding over hundreds to a few thousand hectares. Structural marsh management is a common practice used on both private and public lands, and the objectives include reducing wetland loss, reducing

salinity levels, improving resources for fish and wildlife, and supporting mineral exploration (Cowan et al. 1988). Water-level management may include no active management, holding water within impoundments, a drawdown of water during the spring or summer, and management may be limited due to historical land uses (e.g. rice field levees). At the finest spatial scale, I investigated water depth, open water, edge, vegetation density, and ditches within 100 m of bird point count locations.

In my study, I was particularly interested in the habitat use of secretive marsh birds because many of these birds have apparently declined throughout the United States over the last 30 years and are listed as species of conservation concern (Conway 2011). In particular, the king rail (*Rallus elegans*) is a high conservation priority because of its threatened or endangered status in 12 U.S. states and Canada (Cooper 2008). The objectives of the research were to: 1) determine fine-scale, medium, and broad-scale habitat factors affecting the habitat use of shorebird, wading bird, secretive marsh bird species; 2) test which spatial scale best correlates with marsh bird habitat use and test the combination of spatial scales. I hypothesized bird habitat use would be better explained by a combination of broad, medium, and fine-scale variables compared to the sole use of any single spatial scale.

METHODS

Study Area

All study sites were in the Chenier Plain coastal region of Louisiana and Texas, USA (Figure 3.1). Study sites in Louisiana were at Cameron Prairie National Wildlife Refuge (NWR), Lacassine NWR, Rockefeller State Wildlife Refuge, and White Lake Wetlands Conservation Area. Study sites in Texas included McFadden NWR, Anahuac NWR, and J.D. Murphree

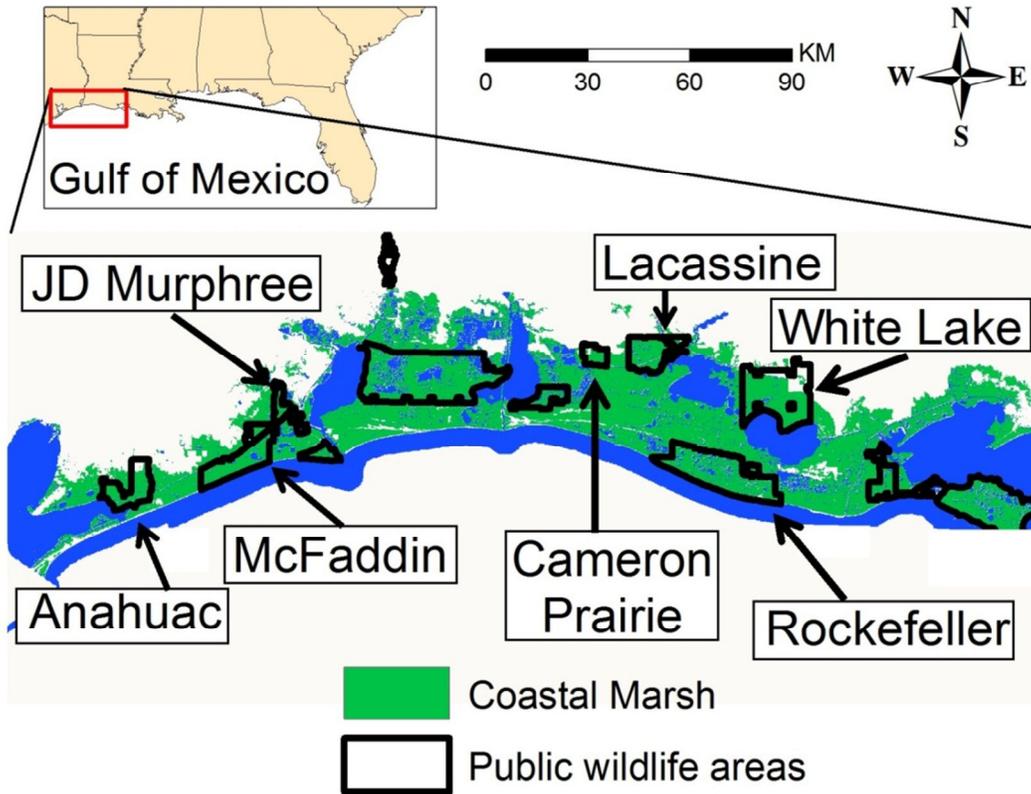


Figure 3.1. Study sites in southwestern Louisiana and southeastern Texas, USA. White Lake, Lacassine, and the majority of Cameron Prairie were fresh marsh. Intermediate marshes included Anahuac, JD Murphree, McFaddin, and Rockefeller.

Wildlife Management Area. Lacassine, White Lake, and Cameron Prairie were primarily characterized as fresh marshes and Rockefeller, JD Murphree, McFaddin, and Anahuac were intermediate, or oligohaline, marshes as described by Visser et al. (2000). The Cheniers, or natural oak ridges, have a geologic origin from sediment deposition and the reworking of sediments from the Mississippi River Delta (Penland and Suter 1989), and the result is numerous landforms, which act as ridges that restrict tidal flow. Water levels are primarily determined by rainfall and seasonal wind-driven tides. Typically, rainfall from November to February typically floods emergent marsh vegetation, and then hot weather and increased evapotranspiration in May and June dries marshes except for permanent ponds and impoundments. Fresh marshes are

dominated by *Panicum hemitomon*, *Typha* sp., and *Sagittaria lancifolia*, while intermediate marshes are dominated by *Spartina patens*, *Phragmites australis*, *Schoenoplectus* sp., *Typha* sp., and *Paspalum vaginatum*.

Marsh Bird Surveys

Bird surveys were conducted between March 9 and June 19 from 2009 to 2011, and surveys included wintering, resident breeding, and migratory breeding birds. March coincided with the start of the resident breeding season and all birds became quiet during the heat of mid-June. Approximately ten survey points were placed along transects with a minimum distance of 400 m between points in 2009 and 2010, and travel between points was performed with motorboat, kayak, pirogues (small canoe), vehicle, and all-terrain vehicle. In 2011, I used a minimum distance of 200 m between survey points to survey interior marsh points by traveling on foot through dense vegetation and 6-8 points were on each transect. Interior surveys were also 250 m from levees or ditches, and transects were placed in areas that had high habitat variability among points according to remote sensing data from a concurrent study. A total of 17 transects were placed in fresh marsh and 18 transects were placed in intermediate marsh. Bird survey points in the Texas sites were replicated in 2009 and 2010 to capture temporal variation in species abundances. Each bird survey point was marked with a painted PVC pipe to maintain a consistent survey location, and a total of six call-back surveys were performed at each point. Throughout the study, I surveyed a variety of management types within fresh and intermediate marshes.

I used a call-back survey technique as described by Conway (2011), since numerous secretive marsh bird studies have found the method to be superior to passive surveying techniques (Conway and Gibbs 2011). Surveys were conducted from 30 minutes before sunrise

until 4 hours after sunrise, and surveys were not conducted during rainfall or with winds >20 km/hr. The order of survey points along each transect was consistently changed to ensure any time of day effect was negligible. Upon reaching a survey point, I surveyed one pre-determined side of the marsh (i.e., 180 degree semi-circle) by auditory and visual observation for 5 minutes during a passive period. I then used a portable MP3 player and 80-90 decibel speakers (at 1 m) to play 30 seconds of marsh bird calls followed by 30 seconds of silence. Calls of black rail (*Laterallus jamaicensis*), American bittern (*Botaurus lentiginosus*), least bittern (*Ixobrychus exilis*), common gallinule (*Gallinula galeata*), king rail, purple gallinule (*Porphyrio martinica*), and pied-billed grebe (*Podilymbus podiceps*) were played in that order. Approximate distances to birds were recorded to the nearest 10 m, and the compass direction was recorded to avoid the double counting of birds. Since I generally could not distinguish male and female marsh birds, all birds observed were counted to represent an index of relative abundance.

Nine observers surveyed birds from 2009 to 2011 with one observer surveying for all three years. Within each year, observers were rotated on all transects to minimize observer bias. Two weeks of intensive training were used in each year to train observers to identify species and estimate distance to birds. 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 my study sites. Therefore, I considered all *Rallus* to be king rail. Ducks were not counted during surveys due to the brief period of their winter residence during my study period. All other waterbirds were recorded during the course of each survey.

Classification of Management Type

Impoundments in the study area varied from structures that held water throughout the bird survey period, March to mid-June, to impoundments where water was drawn down beginning from late March to mid-May. I classified the former as “permanently impounded water” and the latter as "drawdown" according to their typical management strategy. I considered "unmanaged" areas as marsh where direct water manipulation or impoundment was not taking place. Sites with permanently impounded water in intermediate marshes only included impoundments where no water-level manipulation took place, and I did not survey areas where water was held at a shallow level (i.e. 10 cm) throughout the season. A concurrent radio telemetry study examined those types of impoundments. For White Lake and Rockefeller, the drawdowns occurred in approximately mid-May. In contrast, JD Murphree typically draws down water levels starting in late March. All the managed areas differed according to annual conditions and decision-making by managers, but I was primarily interested in the overall differences in these managed marshes compared to unmanaged marshes. Hurricane Ike in the fall of 2008 changed management strategies. For instance, JD Murphree received saline storm surge from Hurricane Ike in their intermediate marsh impoundments and ditches were also clogged. Therefore, JD Murphree held water on impoundments later in the season to dilute saltwater in marshes as much as possible. In 2011, drought conditions at JD Murphree dominated and a true drawdown was not conducted. These annual distinctions were accounted for at a finer spatial scale with measurements such as water depth, vegetation density, and open water.

Fine-scale Variables

Between March 25 and early April 18 of each year, I obtained a snapshot of water depth at each bird survey point. These measurements occurred after the second round of bird surveys

and coincided with the nesting of resident birds, peak calling periods of wintering marsh birds, and the measures directly preceded the arrival of breeding migratory birds in mid-April.

Wintering shorebirds and wading birds were primarily recorded in this early season as well. At each bird survey point, I measured water depth every 10 m along three transects within 50 m of the bird survey point (5 points/transect for a total of 15 water depth measurements). One transect was perpendicular to the survey point and the other two transects were at $\sim 20^\circ$ angles from the point to ensure a characterization of the entire habitat. No water depths were measured within 10 m of a levee or ditch, and water depth transects were extended when levees or ditches impeded measurements. Deep ditches (>50 cm) were not measured because I characterized the ditches elsewhere (see below). Mean water depths from the three transects were calculated for each bird survey point.

In late April, vegetation surveys were conducted at each bird survey point. These surveys corresponded to the previously described water depth transects, and vegetation surveys were conducted 30 m along each water depth transect for a total of three per survey point. Within a 10 m radius (0.03 ha) of each vegetation survey point, I estimated the percent of open water, percent of total vegetation that was dead, and vegetation density. A Robel pole was used to measure the visual obstruction of vegetation as an index of vegetation density (Robel et al. 1970), which was measured directly at the vegetation survey location. Two measures were taken and averaged together, and measurements were recorded at a 1 m height with a distance of 2 m from the pole. At the time of vegetation surveys, I sketched open water and emergent vegetation within a 100 m radius of the each survey point's semi-circle. Sketches were later transferred to ArcGIS 9.3 and the open water /vegetation edge (m/ha) was calculated with a 3x3 Laplacian edge detection filter with a 5 m spatial resolution (ERDAS, Imagine 11.0). I also noted whether a

ditch, or channel, was present (0/1) at the bird survey point. 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 waterbird use of marsh, but I wanted to distinguish ditch use from the marsh vegetation-water interspersion effect.

Analysis

Initial point counts had an unlimited radius, but I used only birds ≤ 100 m from each survey point for habitat analyses (1.57 ha for the surveyed semi-circle) to minimize observer error, minimize detectability differences due to habitat, and to assist with relating birds to fine-scale habitat measures. Since birds in the study sites were wintering, migratory, and breeding birds, I adapted a measure of mean birds per point with the time frame relevant for each species. I used the mean birds per point as an index of relative abundance because I wanted to distinguish high from low habitat use of an area, and surveys had high variability in abundance. Least bittern and purple gallinule are breeding migratory birds in the region, and I used the last three survey rounds to calculate their mean per point. While these species arrived during my third round of surveys, the first birds to arrive may have been passage migrants rather than breeders. Yellowlegs (*Tringa* sp.) and sora rails (*Porzana carolina*) primarily wintered in the area, and I used mean abundance from the first three surveys. American bittern and coot (*Fulica americana*) were included for the first four surveys before their migration was complete. I used all six surveys for black-necked stilts (*Himantopus mexicanus*) and wading birds. I classified *Plegadis* sp. into a single category of dark ibis.

I analyzed species detected at $\geq 25\%$ of point count locations with mean relative abundance, and species present at $\geq 10\%$ of points were analyzed with detection/nondetection as the dependent variable. I only analyzed the gregarious and conspicuous wading birds, since most

wading bird detections were visual. Wading birds generally had erratic abundances, and modeling them with detection/nondetection assisted with statistical analysis. The secretive marsh birds were primarily detected by auditory observations, and it is unlikely detectability differed with vegetation composition. While marsh bird research has used detectability analysis for surveys within a short time frame (Pickens and King 2012), recent evidence suggests the assumption of closure is often violated over the course of a breeding bird season (Rota et al. 2009). For secretive marsh birds, king rail (Chapter 2) and least bittern (Bogner and Baldassarre 2002) can use two home ranges during a breeding season, while shorebirds and wading birds move long distances. Furthermore, the occupancy modeling procedure provide little or no addition to the predictive power of models when detectability is homogeneous (Rota et al. 2011, Pickens and King 2012). Therefore, I interpret detection/nondetection as an index of habitat use and not a form of occupancy. Black-necked stilts were often noisy, but yellowleg shorebirds and the three wading birds modeled were primarily observed visually. I tested for heterogeneity in their detection by examining the distance to bird between marsh types and among treatments. I expected a greater detectability of birds to be indicated by an increase in birds detected at longer distances. Based on the low vegetation density and high open water characteristics (Figure 3.2), I used t-tests to determine whether these four species were detected at greater distances in permanently impounded marsh or fresh marsh.

I used generalized linear models (SAS 9.1; Proc GLIMMIX) to assess the individual effects of broad-scale marsh type, management, and fine-scale habitat variables ($\alpha=0.05$). This first step served to reduce the number of environmental variables, particularly for the fine-scale habitat features. 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 data; the

quasi-Poisson distribution estimates the scale parameter when it differs from one. I did not use site as a random effect, since I tested the effect of marsh type and management type (permanently impounded water, drawdown, unmanaged) at a broad scale. This resulted in replicates within marsh types and management types, and these variables are likely to influence water levels, vegetation, and bird communities. To assess the effect of marsh type and management, year was used as a fixed effect covariate to control for the effect of different years. I tested for the interaction of marsh type and management to determine when management had a differing effect depending on fresh or intermediate marsh types. When management was a significant factor, I used post-hoc contrasts to determine the differences among management types. Contrasts reflected the relative hydroperiod of managed areas. Unmanaged areas were contrasted with drawdown and permanently impounded water, and then drawdown and permanently impounded water were compared ($\alpha=0.05$). I explored the fine-scale data with general additive models (GAMs), which are non-parametric or semi-parametric methods to fit linear and non-linear relationships (Yee and Mitchell 1991). After GAM analysis, I was able to transform predictor variables with quadratic functions, and then conduct the more powerful generalized linear models. Fine-scale habitat variables were first tested with a univariate analysis, and then I performed a multiple regression with a backwards selection procedure for the significant variables. Year was used as a potential explanatory factor for this model. I expected annual differences due to the landfall of Hurricane Ike in the fall preceding my surveys in 2009 ("post-hurricane year"), and the drought year that coincided with interior marsh surveys conducted in 2011. Water depth and proportion of vegetation dead were correlated ($r= -0.53$) and I did not use dead vegetation as a variable. The remaining habitat variables are listed in Table 3.1.

Table 3.1. Habitat variables tested to predict marsh bird abundance or detection/nondetection at multiple spatial scales.

Spatial Scale	Variable	Description
Broad (Dominant vegetation)	Marsh type	Fresh or Intermediate marsh
Medium (Management)	Unmanaged Drawdown Permanently impounded	No levees or water control structures Water drained late March-May Water held on marsh throughout season
Fine-scale (Structure)	Open water (%) Water depth (cm) Vegetation density index (Robel pole: decimeters) Edge (m/ha) Ditch (yes or no)	

To compare models from the three spatial scales and the combination of them, I used Akaike's Information Criteria, corrected for small sample sizes, AIC_c (Burnham and Anderson 2002). Although Lukacs et al. (2007) suggest not mixing AIC analyses with other statistics, the univariate tests served to screen variables, and the AIC analyses were used only to provide evidence for the hypothesis that the combination of spatial scales would produce a better model compared to any single spatial scale. The lowest AIC_c value represents the best model, and all other models are considered relative to the best model. Models within <2.0 of the best model are considered equally plausible, and models with $\Delta > 4.0$ are not considered well supported by the data (Burnham and Anderson 2002). If year was a significant factor retained in the fine-scale analysis, I reported AIC_c results for marsh type and management with year as a covariate; otherwise, year was not included in the final analysis. To determine the amount of variation explained by Poisson models, I followed the approach of Thogmartin et al. (2006) by reporting the Spearman rank correlation between the observed and predicted abundance. For

detection/nondetection models, I used the receiver operator characteristic area under the curve (AUC) to assess the discrimination ability of models (e.g. Gibson et al. 2004, Aldridge and Boyce 2007). The AUC varies from 0 to 1.0, and I interpreted the AUC 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, Pearce and Ferrier 2000, Manel et al. 2001). The receiver operator characteristic is a powerful approach because it is not dependent on animal prevalence or suitability thresholds. For the species modeled with mean abundance, I also report the AUC of a logistic model using the reported habitat variables, but with recalibrated parameter estimates. Means are reported \pm 1SE.

RESULTS

I surveyed 304 points over the three year study period, and a total of 1816 surveys were conducted. A total of 32 waterbird species were recorded during my study (see Table 3.2 for scientific names and abundance). Fresh marshes were characterized by deeper water levels, more open water, and more edge than intermediate marshes (Figure 3.2) The distance to bird analyses found no marsh type differences. The great egret was the only species detected at a greater distance in permanently impounded marsh ($t=-2.3$, $p=0.02$; mean \pm 1 SD: permanently impounded detections: 59m \pm 27, unmanaged/drawdown detections: 72m \pm 22), so I eliminated the great egret from all analyses.

Relative abundance of marsh birds differed greatly between fresh and intermediate marsh (Figure 3.3). Birds associated with deeper, more open water areas were more abundant in fresh marsh. More shallow water species, such as sora, king rail, and least bittern were more abundant in intermediate marsh. Relative bird abundance also differed by management type with a primary gradient of deep water species, such a pied-billed grebe and ibis, being more common in areas

with permanently impounded marsh (Table 3.3; Figure 3.4). The king rail and least bittern were the only birds more abundant in either drawdown or unmanaged areas (Table 3.3; Figure 3.4). King rail, purple gallinule, black-necked stilt, white ibis, and dark ibis were related to the interaction of marsh type and management (Figure 3.4). A variety of fine-scale variables were correlated with bird abundance (Table 3.3; Figure 3.5) and water depth was the most common variable in fine-scale models. The post-hurricane year of 2009 corresponded with decreased detections of dark ibis and white ibis. Common gallinule, king rail, and American coot were less abundant in the drought year of 2011, but yellowleg shorebirds were most common in 2011. The comparison of the three spatial scales consistently showed fine-scale variables provided better models compared to marsh type or management. However, in 11 of 12 species models, the combination of spatial scales was much better than any single spatial scale ($\Delta AIC_c > 2.0$) (Table 3.4). The king rail was the only exception, and the model indicated equal plausibility of models between all three scales and the interaction of marsh type and management. The Spearman correlation between the observed and predicted abundance explained only a moderate amount of variation, but the AUC statistic showed a good ability of the models to distinguish detection and nondetection (AUC=0.76-0.84).

DISCUSSION

The results supported my hypothesis that a combination of broad, medium, and fine spatial scales would better explain the habitat use of marsh birds compared to single-scale models. Although fine-scale habitat variables were frequently the best compared to management and marsh type, my results demonstrate the importance of three distinct spatial scales underlying the distribution of secretive marsh birds, wading birds, and shorebirds. Overall, every model of

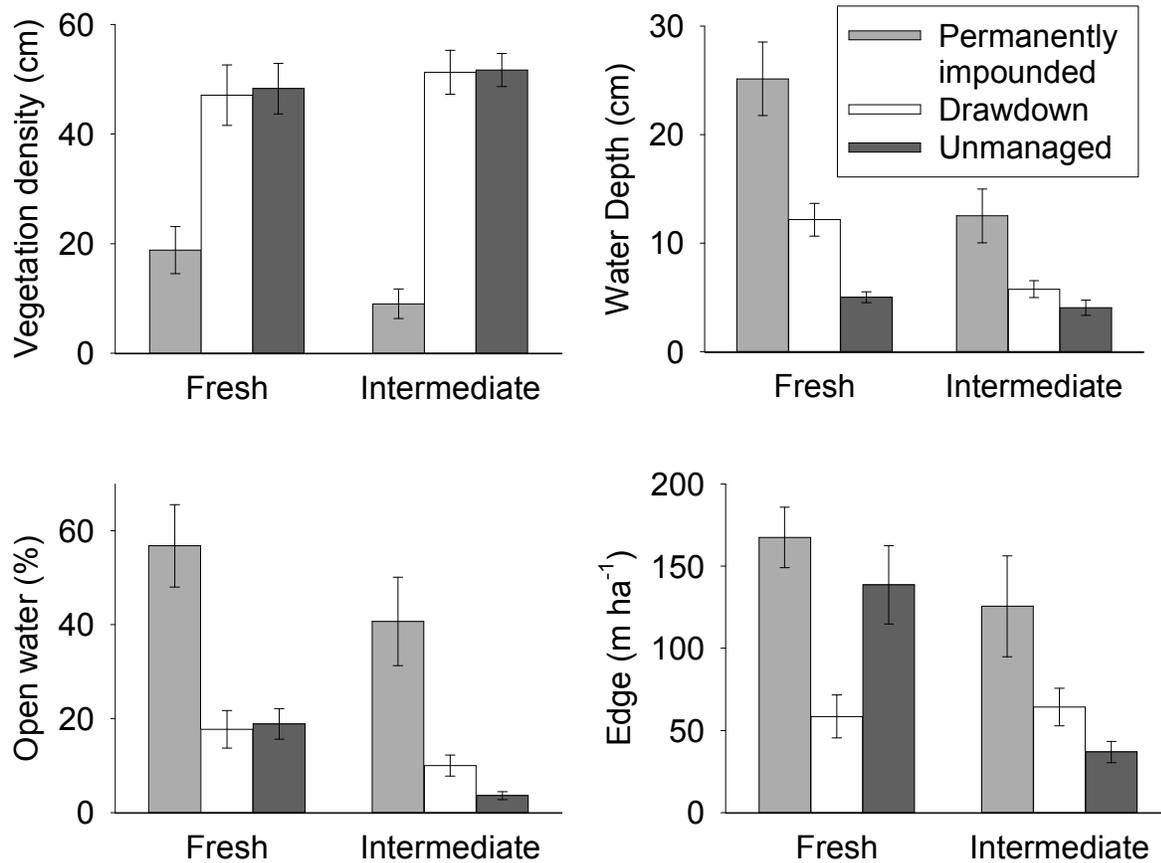


Figure 3.2. Summary statistics of fine-scale variables by marsh type and management in northern Gulf Coast marshes. Water depth was measured in late March to early April; other variables were measured in late April. Means are reported ± 1 SE.

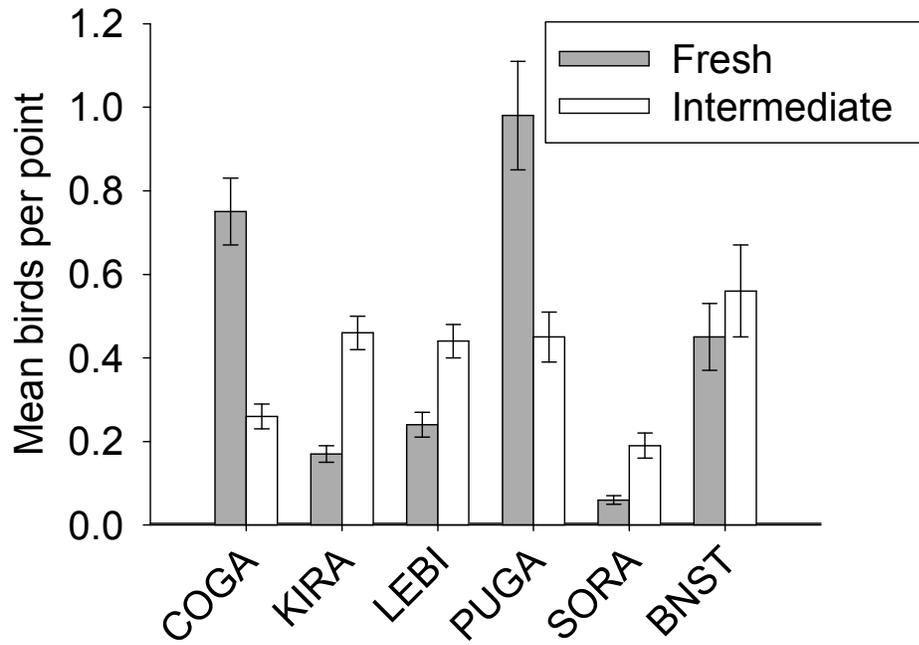
Table 3.2. Total counts of birds observed from 2009 to 2011 within 100 m of a survey point in the coastal marshes of southwest Louisiana and southeast Texas.

Species	Abbreviation	Scientific name	Total counted	Proportion of points
<i>Secretive marsh birds:</i>				
Common gallinule	COGA	<i>Gallinula galeata</i>	867	0.60
King rail	KIRA	<i>Rallus elegans</i>	620	0.57
Least bittern	LEBI	<i>Ixobrychus exilis</i>	391	0.49
Purple gallinule	PUGA	<i>Porphyrio martinica</i>	708	0.48
Sora	SORA	<i>Porzana carolina</i>	127	0.25
American coot	AMCO	<i>Fulica americana</i>	1247	0.18
Pied-billed grebe	PBGR	<i>Podilymbus podiceps</i>	69	0.12
American bittern	AMBI	<i>Botaurus lentiginosus</i>	64	0.12
Virginia rail	VIRA	<i>Rallus limicola</i>	9	0.02
Black rail	BLRA	<i>Laterallus jamaicensis</i>	4	0.01
<i>Wading birds:</i>				
Glossy ibis/white-faced ibis	Dark ibis	<i>Plegadis sp.</i>	1347	0.28
White ibis	WHIB	<i>Eudocimus albus</i>	465	0.18
Great egret	GREG	<i>Ardea alba</i>	630	0.17
Green heron	GRHE	<i>Butorides virescens</i>	101	0.15
Tricolored heron	TRHE	<i>Egretta tricolor</i>	126	0.13
Snowy egret	SNEG	<i>Egretta thula</i>	163	0.07
Great blue heron	GBHE	<i>Ardea herodias</i>	27	0.06
Yellow-crowned night heron	YCNH	<i>Nyctanassa violacea</i>	24	0.05
Roseate spoonbill	ROSP	<i>Platalea ajaja</i>	44	0.04
Little blue heron	LBHE	<i>Egretta caerulea</i>	19	0.03
Cattle egret	CAEG	<i>Bubulcus ibis</i>	28	0.03
Black-crowned night heron	BCNH	<i>Nycticorax nycticorax</i>	8	0.02
Double-crested cormorant	DCCO	<i>Phanlacrocorax auritus</i>	32	0.01

Table 3.2. (continued from above)

Species	Abbreviation	Scientific name	Total counted	Proportion of points
<i>Shorebirds:</i>				
Black-necked stilt	BNST	<i>Himantopus mexicanus</i>	930	0.34
Yellowlegs sp.	Yellowlegs	<i>Tringa sp.</i>	135	0.14
Killdeer	KILL	<i>Charadrius vociferus</i>	50	0.09
Sandpiper sp.	SAND	<i>Calidris sp.</i>	206	0.05
Short-billed dowitcher	SBDO	<i>Limnodromus griseus</i>	198	0.03
Willet	WILL	<i>Tringa semipalmata</i>	8	0.02
Dunlin	DUNL	<i>Calidris alpina</i>	5	0.01
American avocet	AMAV	<i>Recurvirostra americana</i>	2	0.00
Plover sp.	PLOVER	<i>Charadrius sp.</i>	1	0.00
Wilson's snipe	WISN	<i>Gallinago delicata</i>	1	0.00

(a)



(b)

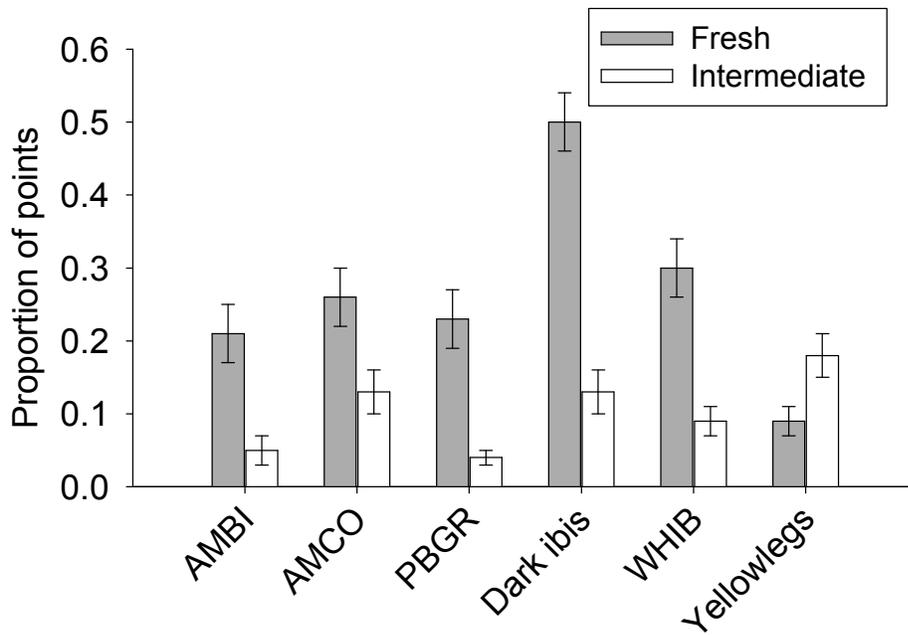


Figure 3.3. Bird survey results from generalized linear models: (a) mean birds per point and (b) proportion of points with bird species detected from fresh ($n=130$) and intermediate marshes ($n=174$). Bars are the mean \pm 1SE. All species are significantly different by marsh type ($\alpha=0.05$) except BNST. See Table 3.2 for species abbreviations.

Table 3.3. The effect of management type on bird abundance or detection/nondetection in fresh and intermediate coastal marsh. Year was a covariate in all management models. Contrasts are reported with $\alpha=0.05$. Quadratic relationships are shown as x^2 and an asterisk (*) signifies the interaction of marsh type and management type. P= permanently impounded water, D=drawdown, U=unmanaged.

Species	Summary	Contrast	Fine-scale Variables
<i>Mean birds per point</i>			
Common gallinule	$F_{2,299}=51.3, p<0.0001$	P>D>U	Depth (+), Edge ² , Open water ² , Vegdens (+), Year
King rail	$F_{2,296}=10.14, P<0.001^*$	Fresh= D>U, P / Int= U>D, P	Vegdens ² , Year
Least bittern	$F_{2,299}=5.50, p=0.005$	U, D>P	Depth ² , Ditch (+)
Purple gallinule	$F_{2,296}=5.04, p<0.01^*$	Fresh= P>D,U / Int=D, P>U	Depth ² , Ditch (+)
Sora	$F_{2,299}=1.60, p=0.20$	NA	Depth ²
Black-necked stilt	$F_{2,296}=4.59, p<0.01^*$	Fresh= P>U / Int=P>D>U	Open water (+), Vegdens (-), Depth (-), Edge ²
<i>Detection/nondetection models</i>			
American bittern	$F_{2,299}=2.25, p=0.11$	NA	Vegdens ² , Year
American coot	$F_{2,299}=17.22, p<0.0001$	P>D, U	Vegdens (-), Depth (+), Edge ² , Year
Pied-billed grebe	$F_{2,299}=11.84, p<0.0001$	P>D, U	Depth (+), Edge (+), Year
Dark ibis	$F_{2,296}=4.58, p<0.02^*$	Fresh= P>D,U / Int= P,D>U	Vegdens (-), Depth (+), Edge ² , Year
White ibis	$F_{2,296}=5.59, P<0.01^*$	Fresh= No effect / Int= P>D,U	Vegdens (-), Edge (+), Year
Yellowlegs	$F_{2,299}=0.29, p=0.75$	NA	Vegdens (-), Depth (-), Year

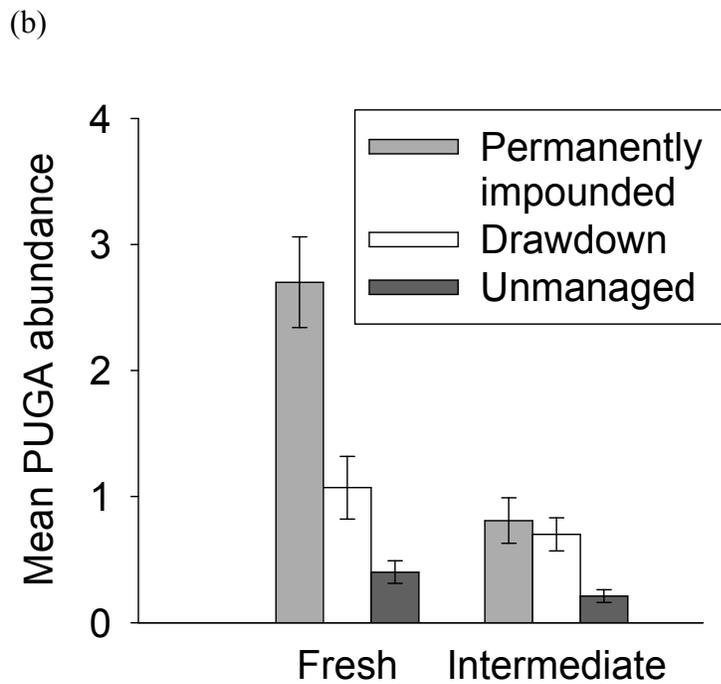
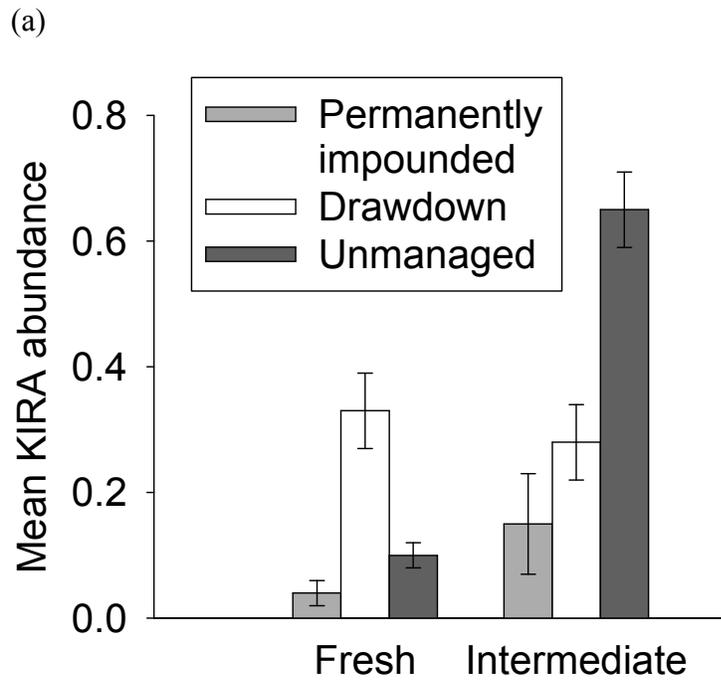


Figure 3.4. The interaction of marsh type and management related to relative abundance of (a) king rail and (b) purple gallinule in Gulf Coast marshes from 2009-2011. The mean is reported with ± 1 SE.

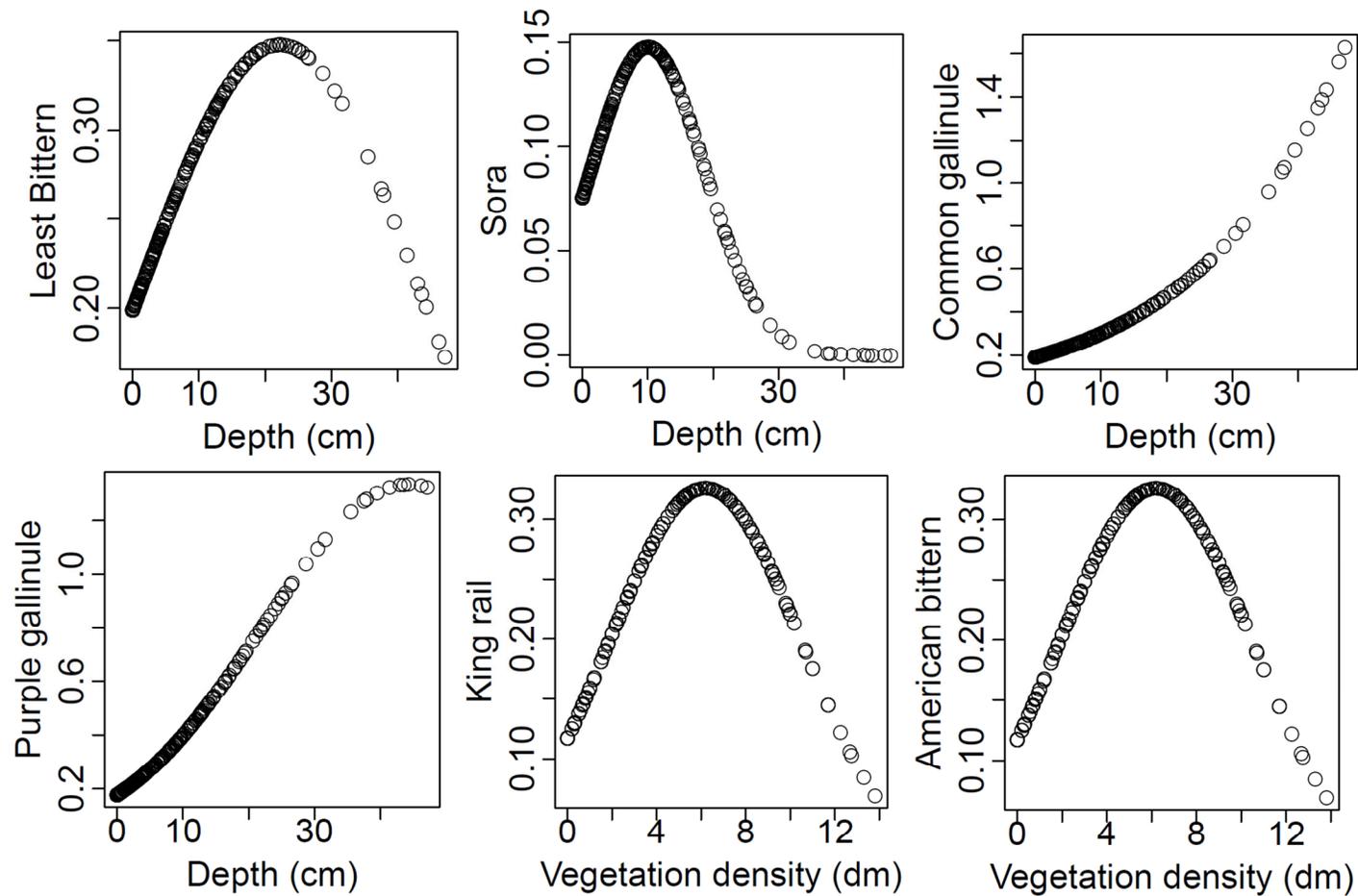


Figure 3.5. A subset of univariate relationships describing the association of fine-scale habitat features to relative bird abundance or probability of detection (American bittern only). The y-axis is the predicted mean abundance of birds given the x-axis variable observed during the study. Mean bird abundance had a Poisson distribution, and therefore, the confidence intervals are not given. All variables were significant at $\alpha=0.05$.

Table 3.4. Generalized linear models with the response of mean birds/point or detection/nondetection. The interaction of management and marsh type are indicated by *. All scales included the significant variables at the three spatial scales. Year was added to models if it was included in the fine-scale habitat model. AUC is the area under the curve statistic and Rho is the Spearman correlation of the observed versus expected abundance.

Species	Spatial Scale	K	AICc	ΔAICc	Rho	AUC	Species	Spatial Scale	K	AICc	ΔAICc	Rho	AUC
<i>Relative abundance models</i>													
Common gallinule	All scales	11	443.1	0.0	0.51	0.76	Purple gallinule	All scales	8	548.3	0.0	0.54	0.78
	Fine-scale	9	463.8	20.7				Fine-scale	5	579.4	31.1		
	Management	4	481.5	38.4				Management*	5	632.4	84.1		
	Marsh type	4	502.3	59.2				Marsh type	3	721.4	173.1		
	Null + year	3	538.0	94.9				Null	2	749.6	201.3		
King rail	All scales	8	377.6	0.0	0.58	0.83	Sora	All scales	5	224.8	0.0	0.33	0.76
	Management*	6	378.6	1.0				Marsh type	3	230	5.2		
	Marsh type	4	393.2	15.6				Fine-scale	4	234.2	9.4		
	Fine-scale	5	397.3	19.7				Management	(not used)				
	Null + year	3	412.3	34.7				Null	2	238.2	13.4		
Least bittern	All scales	7	390.3	0.0	0.52	0.77	Black- necked stilt	All scales	10	449.7	0.0	0.56	0.84
	Fine-scale	5	405.1	14.8				Fine-scale	7	473.1	23.4		
	Marsh type	3	429.0	38.7				Management*	5	620.6	170.9		
	Management	3	429.4	39.1				Null	2	703.4	253.7		
	Null	2	435.1	44.8				Marsh type	3	703.5	253.8		
<i>Detection/nondetection models</i>													
Pie-billed grebe	All scales	7	169.3	0.0	0.86	0.86	Greater & lesser yellowlegs	All scales	6	205.8	0.0	0.80	0.80
	Fine-scale	5	173.9	4.6				Fine-scale	5	209.6	3.8		
	Marsh type	4	204.9	35.6				Management	(not used)				
	Management	4	209.2	39.9				Marsh type	4	233.7	27.9		
	Null + year	3	228.2	58.9				Null + year	3	238.2	32.4		

Table 3.4. Continued from above.

Species	Spatial Scale	K	AICc	ΔAICc	Rho	AUC	Species	Spatial Scale	K	AICc	ΔAICc	Rho	AUC
American bittern	All scales	6	169	0.0		0.82	Dark ibis	All scales	10	229.4	0.0	0.91	
	Marsh type	4	179.4	10.4				Fine-scale	7	242.9	13.5		
	Fine-scale	5	182.8	13.8				Management*	6	267.5	38.1		
	Management	(not used)						Marsh type	4	302	72.6		
	Null + year	3	191.3	22.3				Null + year	3	341.3	111.9		
American coot	All scales	7	213.3	0.0		0.86	White ibis	All scales	8	246.5	0.0	0.82	
	Fine-scale	5	216.2	2.9				Management*	6	254.7	8.2		
	Management	4	252	38.7				Fine-scale	5	260.1	13.6		
	Marsh type	4	279	65.7				Marsh type	4	267.8	21.3		
	Null + year	3	284.6	71.3				Null + year	3	287.2	40.7		

mean birds per point explained a $\rho > 0.50$, and all species models had good discrimination ability ($AUC > 0.70$).

The broad characterization of marsh types was associated with the habitat use of many species and added to variation explained in fine-scale models, despite an apparent overlap with fine-scale variables (Figure 3.2). Common gallinule, purple gallinule, American bittern, coot, pied-billed grebe, dark ibis, and white ibis were more frequently found in fresh marshes dominated by more open water and comparatively deeper water levels. I found the drier intermediate marshes had more king rail, least bittern, and sora. The additional variation described by broad-scale factors may be due to unknown factors or may be indicative of an "area effect" where an increased area of specific suitable wetland habitat increases the overall abundance of birds. In regions with limited wetlands available, clapper rails (*Rallus longirostris*) have been shown to be area limited (Shriver et al. 2004), but relationships with other wetland species are poorly documented. Furthermore, there has been experimental evidence that conspecifics attract each other to potential habitat (reviewed by Fletcher and Sieving 2010), and wetland birds may even select habitat based on the presence of similar species (Ward et al. 2010). Therefore, large areas of suitable habitat may attract more birds.

While secretive marsh birds respond to prescribed burning (Conway et al. 2010) and vegetation management (Poulin et al. 2009), water management has not been explicitly tested. In the Chenier Plain of Louisiana, at least 15% of coastal marsh has some form of water-level management (Cowan et al. 1988), so numerous species are affected. Water-level management, a medium-scale factor in my study, is relevant to a marsh's hydroperiod, including the depth, duration, and seasonality of flooding. In fact, management type may be a better measure of hydroperiod than a snapshot measure of water depth due to the difficulty in measuring temporal

variation of depth over heterogeneous areas. However, without fine-scale variables, classifying all drawdowns into a single category also considerably simplifies management conditions. The majority of bird species were more abundant in marshes where water was being held by impoundments, however, I caution that my study period also coincided with dry conditions in 2010 and 2011. Overall, my results contrast with a winter waterbird study where waterbirds were more abundant in drawdowns compared to areas holding water (Taft et al. 2002). However, their study experimented with a slow drawdown and it was limited to the winter season before a thorough drying of the marsh was complete.

The timing of drawdown can dramatically influence bird species abundance, and in my study, this is reflected in the relative importance of fine-scale variables. For example, least bittern and purple gallinule habitat use was best explained by ditches and water depth measured in late March to April, while marsh type or management type did not predict habitat use as well. By repeating survey locations at JD Murphree in 2009 and 2010, I found both species were far more abundant when water was held on later in the season in 2009 (due to Hurricane Ike and mitigation for saltwater intrusion), and this was reflected in my water depths. The earlier drawdown in 2010 resulted in water depths of zero in most areas. For both these migratory birds, spring water depth explained the variation in relative abundance and year was not a factor in my fine-scale models. The king rail was one of few species where management type, and its interaction with marsh type, better explained habitat use compared to fine-scale variables. King rails were most abundant in the unmanaged intermediate marsh and the fresh marsh drawdown areas, while few rails were in the deeper, permanent water impoundments. In both marsh types, the relationship with management types corresponded with a moderate water depth during the breeding season (Figure 3.2). This is also supported in my concurrent radio telemetry study

(Chapter 2) because king rails consistently used shallowly flooded impoundments in intermediate marsh, which were not surveyed in this study. Overall, the scale of the king rail-habitat relationship is a noteworthy because it has been suggested that the king rail decline in the eastern United States is linked to an increase in deeply flooded wetlands (Hunter et al. 2006). My results support the notion that king rails may be susceptible to broad-scale water level changes.

Weller and Spatcher (1965) described the spatial and temporal succession of waterbirds and their habitat, and this includes the notion that bird diversity is enhanced by a hemi-marsh condition, which is a 50:50 interspersed of open water and emergent vegetation. There is evidence that open water/vegetation edges are positively associated with marsh birds, including rails and bittern species (Rehm and Baldassarre 2007, Darrah and Krementz 2009). Indeed, my study shows 6 of 12 species were positively associated with edge, however, water depth was a more common factor as it was in 9 of 12 fine-scale models. Water depth has previously been shown to be an important predictor for a variety of waterbirds (Colwell and Taft 2000, Bancroft et al. 2002), but my results provide new evidence for the effect of water depth for a variety of secretive marsh birds.

Secretive marsh birds were primarily determined by auditory observations (e.g. king rail detections were 96% auditory), but wading birds were primarily detected visually. Although I initially eliminated small, inconspicuous species, the great egret was also eliminated from the analyses because they were observed at a greater distance in impounded marshes, which could indicate a difference in their detectability. Compared to ibis, the egret was observed to be more solitary, and this may have contributed to its inconsistent observations. Both black-necked stilts and yellowlegs were often observed visually, but both species had distinct calls and were

generally active foragers that commonly flew above vegetation during bird surveys. Vegetation density was included in models of black-necked stilt, coot, white ibis, dark ibis, and yellowlegs. While sparse vegetation could make these birds more visible, the results are also consistent with the ecology of these open habitat species. A quadratic relationship of vegetation density was found for both the American bittern and king rail. For these species, I interpret the upward relationship as the requirement for substantial vegetation density (i.e. open water was measured as a zero on the Robel pole), but the downward trend is indicative of the lack of open water in the three vegetation surveys at each point.

I had annual differences in bird abundance likely due to the impact of Hurricane Ike in southeast Texas and the interior survey points that coincided with a severe drought. Wading birds are known to shift their colonies following hurricanes (Leberg et al. 2007), and I found white ibis and dark ibis were less abundant in the spring following Hurricane Ike. The interior surveys in the drought year of 2011 correlated with a decreased abundance of common gallinule, king rail, and American coot. In contrast, yellowlegs were most abundant during the drought year, possibly because shallow water or muddy areas were more available. Other species, such as purple gallinule and least bittern showed high inter-annual variability in abundance, but water depth appeared to explain this variation. Recent research has found roadside surveys to be adequate when the environment is well represented in such surveys (McCarthy et al. 2012), but the adequacy of exterior wetland bird surveys has largely been ignored and further research is needed. In my study, areas away from roads tended to be drier, and quantifying this variation added to the range of habitat assessed in my surveys. Unfortunately, the interior surveys also coincided with a drought, so the effects are difficult to disentangle. The presence of ditches also explained the relative abundance of least bittern and purple gallinule. Other species were

commonly observed in ditches, such as common gallinule and pied-billed grebes, but other habitat variables were apparently better predictors of their distribution. These observations and results suggest ditches are more likely used if surrounding marsh conditions are appropriate.

Management Implications

My research was consistent with other studies showing fine-scale habitat features are important for marsh birds, but the results also indicate that broad-scale suitable habitat increases the abundance of most species. While wetland area outwardly appears to be a non-factor in the expansive northern Gulf Coast wetlands, my results suggest management areas and broad marsh types affect marsh bird distribution. Wading birds and other deep water species were more abundant in permanently impounded areas. However, the short-term benefit of these habitats should be weighed against the long-term effect on marsh vegetation (e.g. *Typha* expansion). One solution may be to manage for a mosaic of habitats on an annual basis. For king rails, I found abundance increased in fresh marsh when drawdowns occurred, and this corresponds with the suggestion that gradual dewatering provides habitat for rails (Eddleman et al. 1988). These drawdown management areas held water until late spring and the drawdown process allowed for the presence of shallow water ponds when other marsh was dry. In the intermediate marsh sites, drawdown typically left few ponds on the landscape, and king rails were less abundant. In regard to other marsh birds, water depth in late March to mid-April was a factor for many species, including the migratory least bittern and purple gallinule. Therefore, management for these species should consider the timing of migration and breeding; drawdowns conducted before their spring arrival should allow time to reflood the marsh after germination of annual plants for waterfowl.

In conclusion, I have demonstrated that multiple spatial scales affect wetland bird habitat use. Future monitoring and management may benefit from considering broad-scale habitat attributes to inform decisions at a more local scale. Fine-scale vegetation and water characteristics best describe wetland bird habitat, but larger areas of appropriate habitat may increase bird abundance across the landscape.

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CHAPTER 4: A TEST OF THE SPATIO-TEMPORAL TRANSFERABILITY OF HABITAT MODELS: THE CASE OF MIGRATORY AND RESIDENT WETLAND BIRDS

INTRODUCTION

Species distribution models (SDMs) are defined as empirically-derived statistical models that predict the spatial distribution of species with a basis in niche theory (Guisan and Zimmermann 2000). SDMs are increasingly used to gain insights into foundational aspects of ecology, including the niche, species-environment relationships, and the effect of spatial scales. SDMs have also been used to predict the effects of climate change (Hamann and Wang 2006), evaluate land use changes (Seoane et al. 2006), monitor rare species (Guisan et al. 2006), and predict species' invasions. In particular, habitat-based models can be applied to interpolate survey locations and to extrapolate predicted distributions into new regions or into the future (Hirzel and Le Lay 2008). In this regard, the results of SDMs assist to elucidate broad-scale patterns over spatial extents relevant for the conservation and management of biodiversity. The species-environment relationships are often used to predict the distribution of species with the assumption that the distribution is static over space and time.

The spatial and temporal transferability of a model, and a model's generalizability, are an important aspect of SDM applications. Spatial transferability of models to new geographic regions or distinct habitats has shown mixed success. Bamford et al. (2009) demonstrated that models developed for specific localities usually performed better than more general models. However, their study examined generalist birds adapted to nesting in several distinct habitats (e.g. open savanna, water courses, and salt pans for a single species). Other studies have shown spatial transferability to be relatively successful (e.g. Sundblad et al. 2009, Kulhanek et al. 2011). In an extensive study using climate and topography as predictors, Randin et al. (2006) found

geographic transferability of 54 plant species to be relatively weak, but the results were species-specific and model transferability was asymmetrical for many species (i.e. models transferred well from one region to another, but not vice versa). One key to spatial transferability is the directness of the predictor variables to the species. For example, a species may respond directly to vegetation composition, but indirect variables such as climate and topography are often much easier to measure at broad spatial scales. The range of predictor variables in each region is also a factor in spatial transferability. In fact, a few studies have demonstrated that a differing range of abiotic conditions can be responsible for less predictive power when models are transferred to new regions (Murphy and Lovett-Doust 2007, Zharikov et al. 2007). Murphy and Lovett-Doust (2007) also suggest a species' niche may change due to differing habitat conditions causing selection, but more research is needed to explain successful and unsuccessful spatial transferability of models.

Regarding temporal transferability, SDMs typically assume a static environment where species are at equilibrium with factors driving their distribution (Guisan and Zimmermann 2000, Zurell et al. 2009). Non-static environments or species distributions may reflect disturbance events or succession, population dynamics, or an organism's dispersal and movement capability (Austin 2002, Franklin 2010). These factors are especially important when projecting SDMs into the future (Iverson et al. 2011). For example, in an early successional system, Vallecillo et al. (2009) reported that fire history better explained colonization and extinction of birds compared to land cover. Nonetheless, temporal changes in abundance over space has rarely been considered in SDMs (Magurran 2007), and SDMs based on dynamic ecological processes need to be considered whenever possible.

Species' traits have large effects on the accuracy of predictive models and their temporal transferability. Studies of species traits are largely limited to plants and butterflies, but species that are short-lived (Syphard and Franklin 2010), have greater dispersal ability (Dobrowski et al. 2011), and greater mobility (Poyry et al. 2008) are often difficult to accurately model. McPherson and Jetz (2007) investigated numerous species' traits and found species were difficult to model if they had a large geographic range size, were wetland dependent, or were migratory species. While large geographic ranges are commonly associated with generalist species, which have a broad niche, the difficulty involved with modeling migratory and wetland species is less clear. Wetland species tend to be poorly surveyed (McPherson and Jetz 2007) and wetlands are dynamic systems, fluctuating temporally with varying climatic conditions. Wetland management can also modify spatial and temporal habitat conditions via artificial flooding, drawdown, or by stabilizing flooding conditions. Meanwhile, migratory birds are a major conservation concern, yet surprisingly few SDMs have been developed for migratory birds, or have compared models of migratory and resident birds. Migratory birds, and especially wetland birds, are expected to exploit ephemeral resources while resident birds may be more restricted to long-term habitat conditions.

Ephemeral resources are difficult to quantify and SDMs commonly use static land cover maps, elevation, topography, or climatic data as predictors. However, such models ignore temporal changes in the landscape. The mean temperature and precipitation of an area, or elevation class, does not account for annual or seasonal conditions, and the underlying assumption is that recent trends or disturbance events, do not affect species. Modeling with satellite remote sensing data can provide a more direct link between species and the environment, but research has only begun to use the advantages of multi-temporal satellite data

(see Leyequien et al. 2007 for a review, Cord and Rodder 2011). Recent studies have used snapshot images of texture to measure heterogeneity (Bellis et al. 2008), or have simply related bandwidths of satellite data to a species' distribution (Lahoz-Monfort et al. 2010). While these measures can be beneficial for prediction, an approach based on both meaningful indices and multi-temporal satellite data can provide for a greater understanding of species-environment relationships. Mueller et al. (2008) have utilized such an approach by relating a seasonal and inter-annual vegetation index to movements of ungulates, but research is lacking for other ecosystems and species.

In my study, I developed spatially explicit habitat models for two resident and two migratory wetland obligate birds in the coastal marshes of Louisiana and Texas, USA. At a broad spatial scale, wetland birds are related to precipitation both spatially and temporally (Forcey et al. 2011), and management can also determine habitat availability (Murkin et al. 1997). At a local scale, the guild of secretive marsh birds examined in this study are associated with vegetation structure, open water, water depth, and open water-vegetation edge (Lor and Malecki 2006, Rehm and Baldassarre 2007, Jobin et al. 2009) (see Chapter 3). In addition, I explored several other variables related to wetlands, including long-term flooding indices, temporary water, and permanent open water. I examined four bird species in both fresh and intermediate marsh along the Gulf of Mexico, where vegetation composition, open water, water depth, and salinity regimes differ substantially by marsh type (Chapter 3).

I had the following objectives: 1) use satellite remote sensing to develop predictive habitat models for the resident king rail (*Rallus elegans*) and common gallinule (*Gallinula galeata*); the migratory breeding birds, least bittern (*Ixobrychus exilis*) and purple gallinule (*Porphyrio martinica*); 2) test the generality of models and compare the spatial transferability of

models between fresh and intermediate marsh types; 3) correlate the predicted spatial distribution of birds among years to determine their temporal transferability; and 4) determine if marsh type or migratory status affect temporal transferability. I hypothesized that models would be spatially transferable between fresh and intermediate marsh because marsh birds are well known to select for a limited number of habitat variables (e.g. open water-vegetation edge, water depth), and the assumption is the bird-habitat relationship is the same in all wetlands. I also hypothesized that the predicted spatial distribution of the resident king rail and common gallinule would be more correlated among years compared to the migratory least bittern and purple gallinule.

Comparatively, migratory birds should exploit more ephemeral resources, while resident birds should relate to long-term habitat conditions.

METHODS

Study Area

All sites were in the Chenier Plain coastal region of Louisiana and Texas, USA (Figure 4.1). Study sites in Louisiana were located at Cameron Prairie National Wildlife Refuge (NWR), Lacassine NWR, Rockefeller State Wildlife Refuge, and White Lake Wetlands Conservation Area. Study sites in Texas included McFadden NWR, Anahuac NWR, and J.D. Murphree Wildlife Management Area. Lacassine NWR, White Lake Conservation Area, and Cameron Prairie NWR were primarily characterized as fresh marsh, and dominant vegetation species were *Panicum hemitomon*, *Typha* sp., and *Sagittaria lancifolia*. The fresh water flow of these sites has been modified by channels, levees, and water control structures to prevent salinity intrusion and to hold water for rice agriculture to the north (Gunter and Shell 1958). Rockefeller Refuge, JD Murphree WMA, McFadden NWR, Anahuac NWR were categorized as intermediate marshes. I

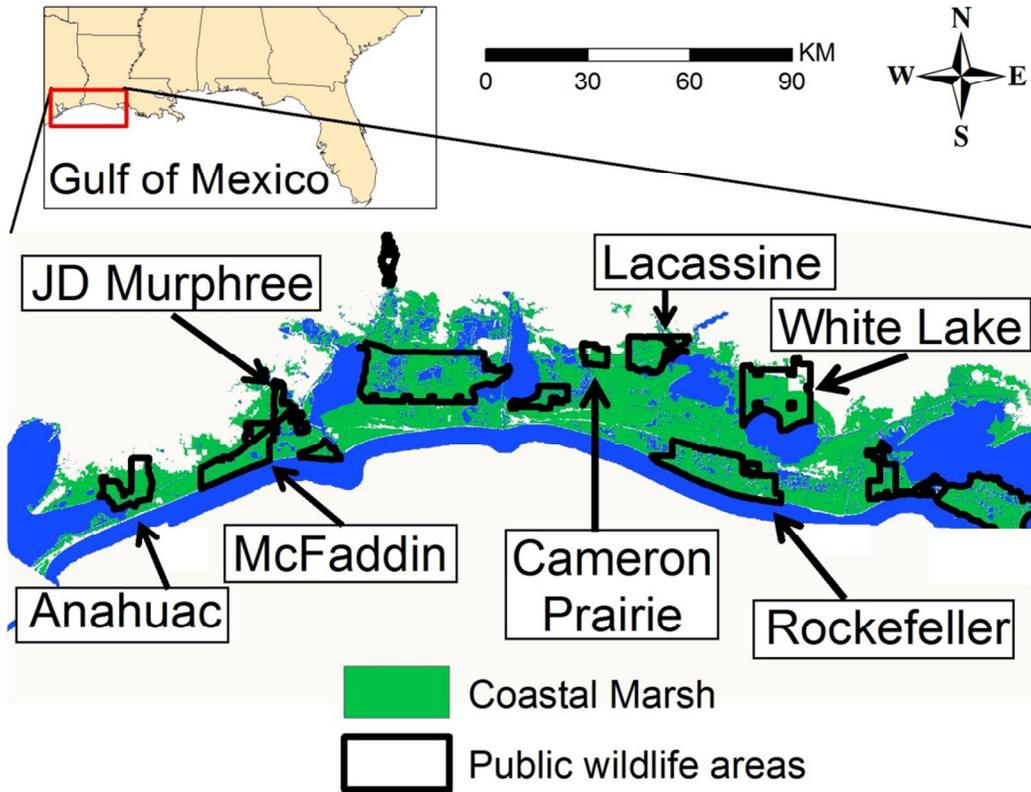


Figure 4.1. Study sites in coastal Louisiana and Texas, USA. White Lake State Conservation Area, Lacassine National Wildlife Refuge (NWR), and Cameron Prairie NWR are fresh marsh, while Rockefeller, McFaddin NWR, and Anahuac NWR are intermediate, or oligohaline, marsh.

followed the classification of intermediate marsh by Visser et al. (2000), which included three oligohaline marsh communities. The primary vegetation in intermediate marsh included *Spartina patens*, *Phragmites australis*, *Schoenoplectus* sp., *Typha* sp., and *Paspalum vaginatum*. Water levels are primarily determined by rainfall, seasonal wind-driven tides, water-level management, and the Cheniers, or oak ridges, prevent substantial tidal influence. Rainfall in the winter months (November-February) typically floods marshes, and then low precipitation and increased evapotranspiration dries most marshes by May or June with the exception of permanent ponds and impoundments. The geographic range of study sites represent one of the steepest gradients of a precipitation: evaporation ratio in the United States (see Woo and Winter 1993 in Mitsch and

Gosselink 2007). Hurricane Ike impacted the coast in the fall of 2008, and a severe drought occurred in 2011 (-45 cm from normal January-May precipitation), so conditions varied substantially both spatially and temporally.

Marsh Bird Surveys

From 2009 to 2011, bird surveys were conducted between March 9 and June 19 of each year (also outlined in Chapter 3). March coincided with the start of the resident breeding season and migratory breeding birds arrived by late April. Over 100 point locations were surveyed each year ($n=304$), and each point was surveyed six times per year; bird survey locations in Texas were replicated in 2009 and 2010 to capture temporal variation in species abundances.

Approximately ten survey points were placed along transects with a minimum distance of 400 m between points in 2009 and 2010, and travel between points was performed with motorboat, kayak, pirogues (small canoe), vehicle, and all-terrain vehicles. In 2011, I used a minimum distance of 200 m between survey points to enable travel by foot for interior marsh surveys. Interior surveys were 250 m from levees or ditches, and transects were placed in areas that had high habitat variability among points according to preliminary remote sensing indices. A total of 17 transects were placed in fresh marsh and 18 transects were in intermediate marsh. Each bird survey point was marked with a painted PVC pipe to maintain a consistent survey location.

I used a call-back survey technique as described by Conway (2011), since numerous secretive marsh bird studies have found the method superior to passive surveying techniques (Conway and Gibbs 2011). Surveys were conducted from 30 minutes before sunrise until 4 hours after sunrise; surveys were not conducted during rainfall or with winds >20 km/hr. The order of survey points along each transect was consistently changed to ensure any time of day effect was negligible. Upon reaching a survey point, I surveyed one pre-determined side of the marsh (i.e.,

180 degree semi-circle) by auditory and visual observation for 5 minutes during a passive period. I then used a portable MP3 player and 80-90 decibel speakers (at 1 m) to play 30 seconds of marsh bird calls followed by 30 seconds of silence. Calls of black rail (*Laterallus jamaicensi*), American bittern (*Botaurus lentiginosus*), least bittern, common gallinule, king rail, purple gallinule, and pied-billed grebe (*Podilymbus podiceps*) were played in their respective order. Approximate distances to birds were recorded to the nearest 10 m, and the compass direction was recorded to avoid double counting birds. Since I generally could not distinguish male and female marsh birds, all birds observed were counted to represent an index of relative abundance. Nine observers surveyed birds from 2009 to 2011 with one observer surveying for all three years. Within each year, observers were rotated on all transects to minimize observer bias. At least two weeks of intensive training were used in each year to train observers to identify species and estimate distance to birds.

Development of Indices and Classifications from Landsat TM 5

I used satellite remote sensing data from Landsat Thematic Mapper 5 (Landsat) to quantify the hydrological and vegetative characteristics of the coastal marsh. Landsat imagery was obtained when clouds were minimal (<15% of scene) from the individual study years and additional years for the long-term indices (see below). One scene required to estimate spring habitat variables in 2009 required an unsupervised classification and buffer analysis to eliminate clouds. I included all coastal marsh within the extent of the study area (Path 24 and 25, Row 39), and later excluded marsh types as needed. Satellite imagery was processed with ERDAS Imagine software (Norcross, GA), and I used radiometric corrections to standardize images among seasons and years.

I developed twelve habitat variables related to either single snapshots of marsh habitat in the spring (April 28- June 28), winter (November 26-February 20), or with long-term hydrological characteristics (Table 4.1). A common index of vegetation cover is the normalized difference vegetation index: $NDVI = (Band\ 4 - Band\ 3) / (Band\ 4 + Band\ 3)$. The NDVI measures greenness, and has been correlated with biomass (Xie et al. 2009) and vegetation cover (Nagler et al. 2009). I used the NDVI from two distinct time frames: Nov. 26 - Feb. 20 (winter) and April 28 - June 28 (spring). Steyer (2008) showed NDVI values to be relatively stable during these time frames. I only included winter NDVI as a variable for the king rail because I observed substantial mortality of king rails in winter (personal observation), and the winter NDVI was unlikely to affect the common gallinule or the migratory species. I removed classified open water from the NDVI layers, and the NDVI coefficient of variation measured vegetation heterogeneity.

The identification of water from Landsat imagery has been demonstrated by numerous studies quantifying flooding and wetland area (Sakamoto et al. 2007, Hui et al. 2008, Reis and Yilmaz 2008). I used the modified normalized difference water index (MNDWI) for water-related variables (Xu 2006, Hui et al. 2008). This index was developed to distinguish water from land as: $MNDWI = (Band\ 2 - Band\ 5) / (Band\ 2 + Band\ 5)$, and I also used the MNDWI as a categorical variable by identifying a threshold to classify open water. Verification of the open water threshold was performed by repeated evaluation of known lakes, permanent ponds, linear ditches, and canals observed from aerial photography. I quantified open water-vegetation edge based on a convolution filter in ERDAS Imagine (Laplacian filter, 3x3 cells). The filter quantifies the differences between adjacent cells and sharp differences are classified as edge (i.e., interface of open water and vegetation). Edge variables were transferred to vector format and

Table 4.1. Landsat variables tested in habitat models to predict migratory and resident coastal marsh birds. Variables are reported from a neighborhood analysis within 1000 m² of a survey point. The overall variable range and the median for both marsh types are reported for 2009-2011. SD=standard deviation, CV= coefficient of variation, M=variables developed from multi-temporal imagery.

Variable	Description	Variable Range	Median Fresh	Median Intermediate
Open water	Spring open water (April 28-June 28)	0.00-1.00	0.23	0.28
Permanent water ^M	Classified as water in $\geq 70\%$ of images	0.00-0.94	0.10	0.17
Temporary water ^M	Spring open water - permanent water	0.00-0.67	0.05	0.04
Edge (km/km ²)	Spring open water/vegetation boundary	0.00-0.61	0.17	0.18
Wetness Index	Spring MNDWI (April 28-June 28)	-0.50- -0.07	-0.30	-0.30
Wetness index CV	MNDWI spatial heterogeneity	-0.86- -0.06	-0.22	-0.19
Winter NDVI	NDVI (November 26-February 20)	0.00-0.58	0.21	0.32
Spring NDVI	NDVI (April 28-June 28)	0.21-0.66	0.43	0.47
Spring NDVI CV	NDVI spatial heterogeneity (April 28-June 28)	0.04-0.52	0.15	0.19
Hydro-Index ^M	Mean wetness index over 5 years	0.35-0.06	-0.20	-0.22
Hydro-Index SD ^M	Hydro-Index spatial heterogeneity	0.03-0.25	0.09	0.07
SDT Hydro-Index ^M	Wetness index heterogeneity over time (5 years)	0.06-0.34	0.16	0.15

were calculated in length of edge per km². After removing open water from the image, the remaining MNDWI was used as a continuous wetness index for emergent marsh. Examination of the wetness index showed concentric circles surrounding open water. The heterogeneity of wetness was quantified with the coefficient of variation.

Long-term wetland indices were developed from 16 images in Texas and 16 in Louisiana (Appendix A). To develop variables that reflected management and temporal variation, Landsat images were divided into winter (November-February), spring (March-June), and summer (July-October) seasons. A maximum of two scenes were obtained for each season from 2006-2010; all images were separated by >30 days to maximize information content. Permanent open water was defined as water classified in >70% of all images obtained; this criteria accounted for infrequent droughts and classification errors. Temporary water was estimated as spring open water minus the permanent open water. A long-term wetness index, or "hydro-index," was derived from the mean MNDWI of all the images to represent the duration and frequency of flooding of the wetlands. I removed permanent open water from the hydroperiod index to ensure the index reflected emergent marsh conditions. Long-term heterogeneity in flooding over time was estimated with the standard deviation of all the wetness indices. Spatial heterogeneity in long-term wetness was estimated with the standard deviation of the hydro-index over the appropriate spatial scale.

I further developed remote sensing variables with the Spatial Analyst extension in ArcGIS 9.3 with 180m² and 1000 m² neighborhood analysis for each cell, and variables had an initial spatial resolution of 30 m². The two spatial scales represented the finest-scale analysis possible and a larger spatial scale that was previously found relevant to king rails in an agricultural landscape (Pickens and King 2012). During model development, a 100 m² spatial

resolution was maintained, and data was projected to WGS_1984 UTM Zone 15N. Interpolation of models in Louisiana were conducted using the marsh type classification by Sasser et al. (2008), and the Texas study area was classified as entirely intermediate marsh with the exception of localized fresh marshes.

Analysis

Initial point counts had an unlimited radius, but I used only birds ≤ 100 m from each survey point for habitat analyses (1.57 ha for the surveyed semi-circle) to minimize observer error and minimize detectability differences due to habitat. Since birds in the study sites were migratory and resident birds, I adapted a measure of mean birds per point with the time frame relevant for each species (3 or 6 survey visits, respectively). I used relative abundance as an index of habitat use because there was high variability in my dataset, and I wanted to distinguish high and low habitat use. The marsh birds were primarily detected by auditory observations, and it is unlikely detectability differed with vegetation composition. In addition, least bittern (Bogner and Baldassarre 2002) and king rail (Chapter 2) are known to use two distinct home ranges during a season, so populations are not closed as required for detectability analysis. Furthermore, the occupancy modeling procedure provides little or no addition to the predictive power of models when detectability is homogeneous (Rota et al. 2011, Pickens and King 2012).

To minimize multi-collinearity problems, I used general additive models (GAMs) to screen variables with univariate tests. GAMs are nonparametric or semi-parametric modeling techniques that are capable of modeling nonlinear trends using smoothing splines (Yee and Mitchell 1991, Hastie et al. 2009). I used cubic regression splines and a restricted maximum likelihood approach to construct smoothers with a maximum of four degrees of freedom to minimize overfitting the data. In all GAM analyses, I used a quasipoisson distribution with a log

link. When a variable was significant at both the 180m² and 1,000m² spatial scales, I performed a backwards selection procedure with the two-term model ($\alpha=0.05$), and examined the results for multi-collinearity problems. I also performed a two-term analysis with variables that were highly correlated ($r>0.80$). When temporary water, permanent water, and open water ($r\sim 0.70$) were all significant at the same spatial scale, I discarded open water since it was a combination of the other two variables.

With the variables screened, I performed the final analysis with multivariate adaptive regression splines (MARS) (Friedman 1991, Hastie et al. 2009). MARS fits non-linear functions with piecewise linear regression splines, or basis functions, and the method has shown good discrimination ability in species distribution modeling (e.g. Leathwick et al. 2005, Heinanen and von Numers 2009). MARS functions are also easier to implement in GIS mapping compared to nonlinear functions, such as GAM. MARS analyses are similar to both stepwise regression and recursive partitioning procedures found in classification and regression trees (CART), but MARS uses linear splines instead of simple thresholds. First, a forward selection procedure determines the most relevant variables, and their associated breakpoints, or knots, where the residual sums-of-squares are minimized with least-squares regression. Models are generally overfit during the forward pass, and a backwards pass is accomplished by using a generalized cross-validation procedure that analyzes model subsets and removes variables that cause the least reduction in model residuals. During the backwards pass, variable importance is calculated based on the reduction of the residual sums-of-square during variable removal. After MARS models were formed for each species, I tested for a year effect, and included it in final models when the effect added $>5\%$ of the deviance explained to models. This strategy maximized the interpretation of variable effects and allowed inter-annual effects to be realized. A generalized linear model

(McCullagh and Nelder 1989) with a Poisson distribution was used to estimate coefficients for basis functions, and I used the $\log(n+1)$ of mean relative abundance for the dependent variable.

To calibrate and validate habitat models, I split the data into training and validation data sets by randomly selecting 65% of fresh and 65% of intermediate marsh points for training. After determining the deviance explained (D^2) of the training model, equivalent to an r^2 for general linear models, the other 35% of data were used for model validation. To measure model validation predictive power, I used a Spearman rank correlation (R_s) between the observed and expected mean relative abundance. I initially fit species' models with all the training data, and marsh type was used as a potential variable. Second, I developed separate models with only fresh or intermediate marsh training data. I then tested the transferability of models between marsh types (i.e. fresh model to intermediate marsh; intermediate model to fresh marsh). During transferability tests, I maintained the sample size of validation data to make results comparable between marsh types. For example, the fresh marsh model was transferred to the validation dataset of intermediate marsh. All species' models were mapped with the MARS basis functions.

To assess temporal transferability among the three years, I sampled the predicted relative abundance of each 100 m² cell for each species in each year. With the entire extent of each marsh type included, I used a Spearman correlation to quantify spatial changes in predicted relative abundance. For the temporal analysis, I only analyzed data available for three consecutive years. Texas intermediate marsh west of McFaddin was excluded since the 2011 image was unavailable, and I excluded Louisiana intermediate marsh because of clouds in this section of the 2009 image. I did not perform bird surveys in the missing Texas scene during 2011, so statistical models were unaffected. A preliminary analysis showed Louisiana intermediate marsh correlations for 2009-2010 were similar to the Texas intermediate marsh. To

test factors affecting the correlation of bird distributions among years, I performed an ANOVA with the three Spearman correlations (2009-2010, 2010-2011, 2009-2011) for each species within each marsh type ($n=24$), and marsh type and migratory status were used as predictor variables. I used a simple linear regression to test if the overall mean predicted abundance of species explained variation in temporal correlation. I also performed a post-hoc analysis on areas with three consecutive years of data to determine if temporary water differed by marsh type. I sampled the proportion of temporary water within a 1000 m² neighborhood for the three years of study, and samples were taken every 1000 m (fresh: $n=1183$, intermediate $n=830$ per year).

Spatial autocorrelation can result in decreased precision of parameter estimates, which can result in Type I errors (Legendre 1993) and bias model selection by favoring broad-scale variables (Diniz et al. 2003). For the purposes of prediction, autocorrelation may not be problematic, but the inference of important predictors may be biased (Franklin 2009). I tested for the existence of spatial autocorrelation in the residuals of models with the Moran's I statistic. I used spatial weights quantified by the inverse Euclidean distance within a 5000 m neighborhood. The Moran's I was calculated with a Monte Carlo simulation with 1000 perturbations. The Moran's I statistic ranges from -1 (perfect dispersion) to +1 (perfect correlation), and zero represents no spatial autocorrelation. I used R (R Development Core Team) and the packages 'earth', 'mgcv', and 'spdep' for statistical analysis.

RESULTS

Model Generality and Spatial Transferability

In the three years of surveys, I recorded 620 king rail, 867 common gallinule, 708 purple gallinule, and 391 least bittern. The range of deviance explained by models ranged from 36-79% (Table 4.2), and the more open water species, the gallinules, showed greater predictive power.

The general marsh models, based on both marsh types combined, explained a moderate amount of variance, and consistently had a positive correlation with the validation data within marsh types. However, the validation results revealed 6 of 8 models had higher predictive power for marsh-specific models. Overall, the validation results indicated poor transferability of models between marsh types (Table 4.2). Of the eight tests of spatial transferability, on five occasions the validation predictive power (R_s) was reduced by over 60%, one was reduced by 44%, and the other gained a small amount of predictive power (7%). Validation results showed good predictive ability of models (Figure 4.2, 4.3), but the variance explained was generally less than the training data.

Habitat Characteristics

The 1 km² spatial scale variables were selected on 19 occasions, while the 180 m² scale variables were selected on 13 occasions. Overall, variable selection differed substantially between fresh and intermediate marsh for each species (Figures 4.4-4.7). For all models combined, 32 variables were selected and 11 of these were found in a species' fresh and intermediate marsh model (disregarding scale). However, even in cases where the same variable was relevant in both marsh types, the species-environment relationship was often substantially different. Birds in intermediate marsh selected for long-term variables, such as the hydro-index or permanent open water, for a total of 31% of the variables. Meanwhile, fresh marsh models were characterized with only 19% these long-term variables. Overall, temporary water was the most frequently selected variable and was in six of eight species models. Edge was found in four models, and the heterogeneity of both wetness and vegetation greenness were common in models. The Moran's I statistic revealed king rail, least bittern, and common gallinule had no

Table 4.2. Results of MARS analysis relating Landsat habitat variables to relative bird abundance (mean birds per point). Marsh type is the origin of the model: fresh, intermediate, or both marsh types. The training D^2 is the percent deviance explained in the training data. The validation results state the Spearman correlation, R_s , for each model by marsh type. Bold R_s values are the best models for each marsh type.

Species	Marsh type	No. Variables	Training D^2	Validation Fresh (R_s)	Validation Intermediate (R_s)
King rail	Fresh	3	37%	0.39	0.24
	Intermediate	5	53%	-0.21	0.43
	Combined	7	54%	0.01	0.41
Least bittern	Fresh (w/year)	4	46%	0.39	0.08
	Intermediate	4	42%	0.13	0.34
	Combined	4	36%	0.24	0.52
Common Gallinule	Fresh	5	79%	0.85	0.32
	Intermediate	3	34%	0.26	0.30
	Combined	7	61%	0.82	0.31
Purple Gallinule	Fresh	5	78%	0.76	0.19
	Intermediate	4	66%	0.37	0.54
	Combined	6	48%	0.74	0.38

spatial autocorrelation in either marsh type. Purple gallinule only showed spatial autocorrelation in intermediate marsh, but the Moran's I statistic was very low (Moran's $I=0.07$, $p=0.02$).

For king rails, temporary water was the most important predictor in fresh marsh, and the relationship with open water (temporary + permanent) was strikingly different in intermediate marsh (Figure 4.4). In fresh marsh, king rails were positively related to the winter NDVI, and both marsh types showed king rails were negatively correlated with spring NDVI. Spatial and temporal heterogeneity of wetness dominated in the intermediate marsh model (3 of 5 variables). King rails selected for increased spatial heterogeneity in wetness in the spring and long-term indices. Furthermore, king rails were negatively correlated with long-term temporal

heterogeneity in wetness. Upon visual inspection, high temporal heterogeneity was indicative of marshes managed to hold water in the winter and then drained in the spring to produce annual plants for wintering waterfowl (i.e. drawdown management).

The least bittern intermediate marsh model was developed from fresh and intermediate marshes combined, and marsh type itself was not included in the model. Year explained 7% of the deviance, but the effect created an unrealistic response curve, which lowered the validation results. Therefore, I did not include the year effect. Least bitterns in intermediate marsh increased with more edge and temporary water. In fresh marsh, the year effect explained 26% of the variance in least bittern relative abundance. Least bitterns in fresh marsh were negatively associated with the wetness index, but positively associated with open water and edge.

The common gallinule and purple gallinule had several common habitat attributes. For both species, temporary water was the most important variable in both marsh types (Figure 4.5, 4.7). The two species responded to temporary water in fresh marsh with a sharp increase in abundance from approximately 10-30% temporary water, and then followed with a sharp decline in relative abundance. Upon inspection of GIS maps, this corresponded to the edge of temporary water bodies. Meanwhile, the bird-temporary water relationship in intermediate marsh was basically a positive correspondence. Permanent water was in both species' fresh marsh models, but was not a factor in either intermediate marsh model. Both species had a negative correlation with the heterogeneity of vegetation (NDVI CV) in fresh marsh, and this relationship probably corresponded with areas with more permanent water, and therefore, less vegetation diversity. Edge had a positive influence on both species in intermediate marsh,

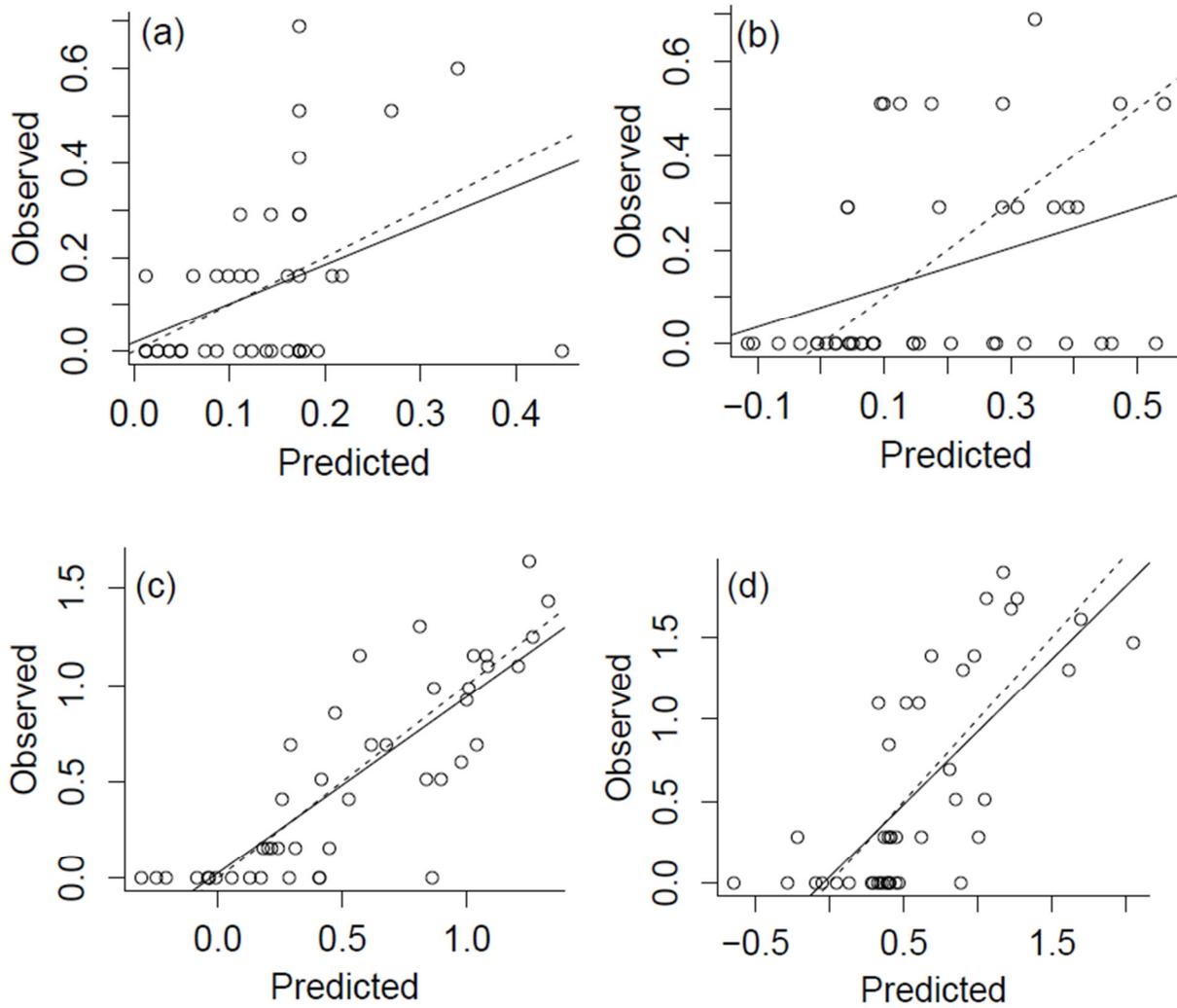


Figure 4.2. Observed versus predicted mean relative abundance $\log(y + 1)$ of marsh bird validation data in fresh marsh. The dashed line references a perfect 1:1 correlation, and the solid line references the least-squares regression of the validation data. (a) king rail (*Rallus elegans*), (b) least bittern (*Ixobrychus exilis*), (c) common gallinule (*Gallinula galeata*), (d) purple gallinule (*Porphyrio martinica*).

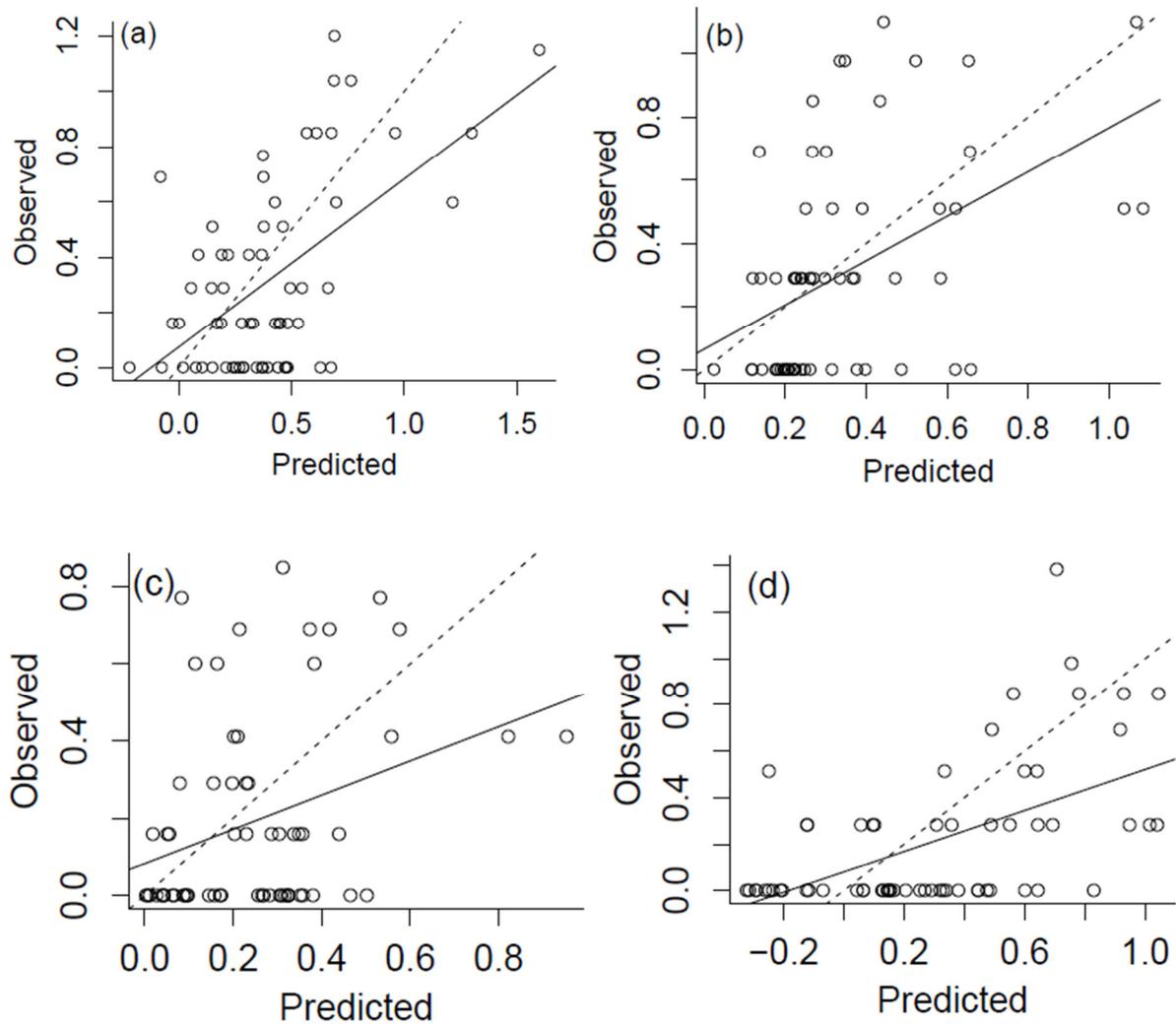
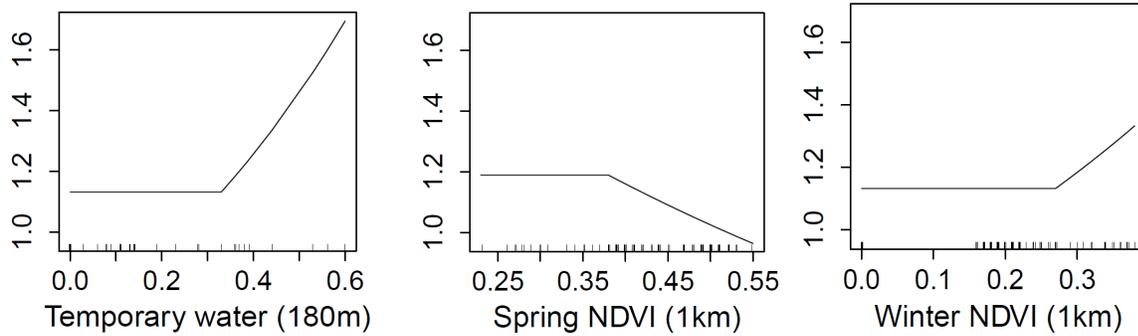


Figure 4.3. Observed versus predicted mean relative abundance $\log(y + 1)$ of marsh bird validation data in intermediate marsh. The dashed line references a perfect 1:1 correlation, and the solid line references the least-squares regression of the validation data. (a) king rail (*Rallus elegans*), (b) least bittern (*Ixobrychus exilis*), (c) common gallinule (*Gallinula galeata*), (d) purple gallinule (*Porphyrio martinica*).

(a) Fresh marsh



(b) Intermediate marsh

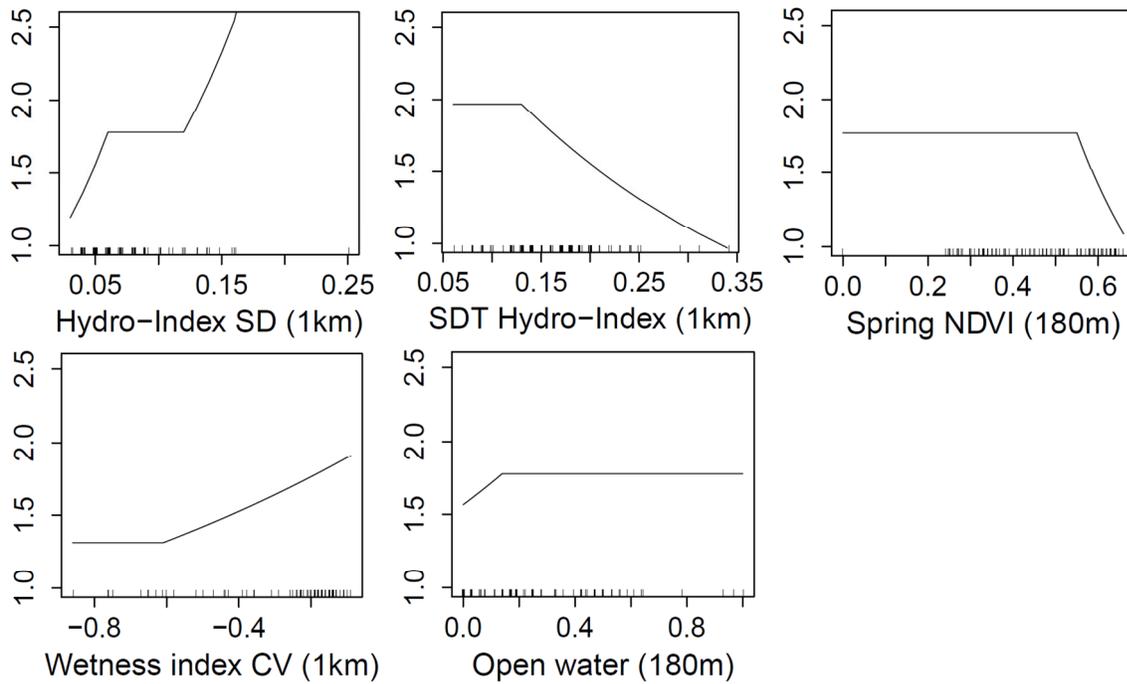
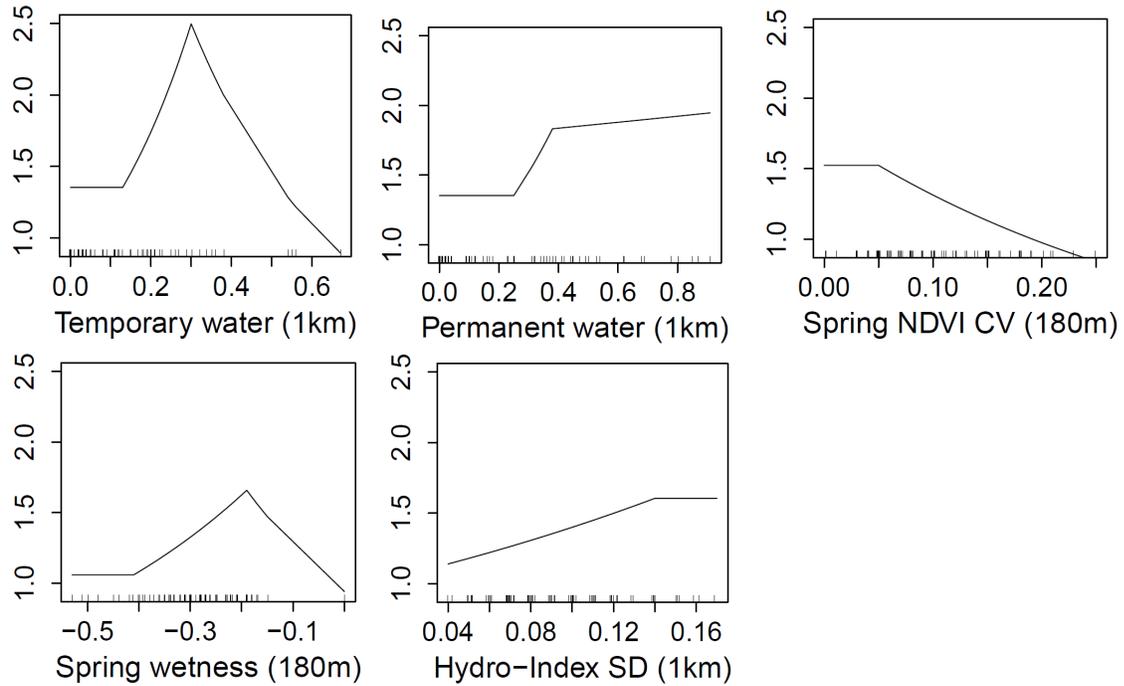


Figure 4.4. Habitat models for the log (y+1) mean relative abundance (y-axis) of the resident king rail (*Rallus elegans*) within (a) fresh marsh and (b) intermediate marsh. Variables are in order of highest importance (left to right). Rug plots show the distribution of x-axis data.

(a) Fresh marsh



(b) Intermediate marsh

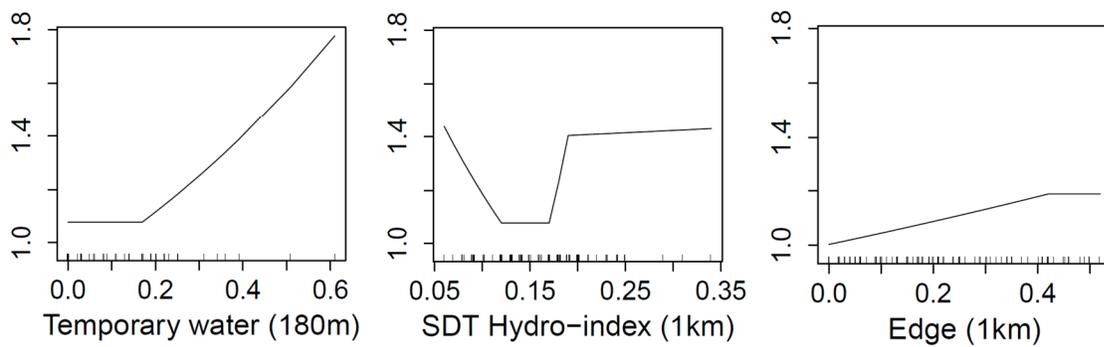
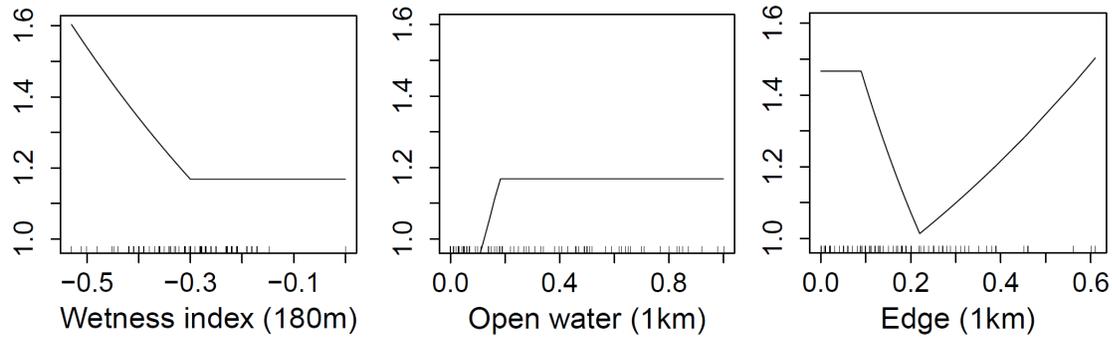


Figure 4.5. Habitat models for the log (y+1) mean relative abundance (y-axis) of the resident common gallinule (*Gallinula galeata*) within (a) fresh marsh and (b) intermediate marsh. Variables are in order of highest importance (left to right). Rug plots show the distribution of x-axis data.

(a) Fresh marsh



(b) Intermediate marsh

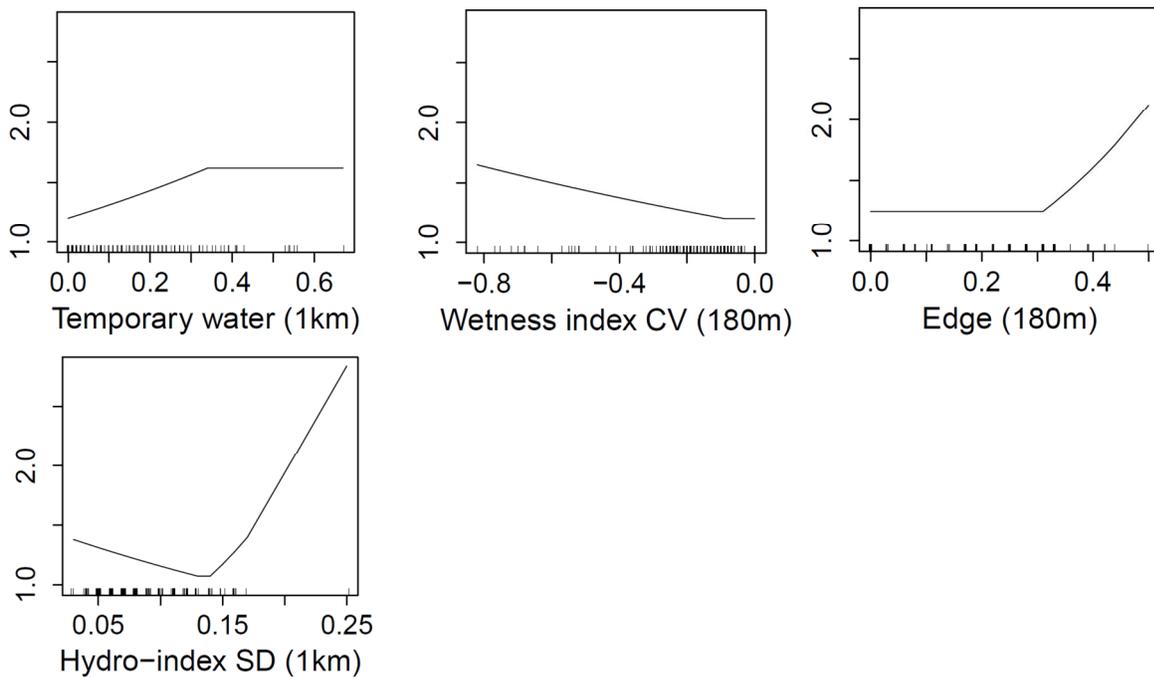
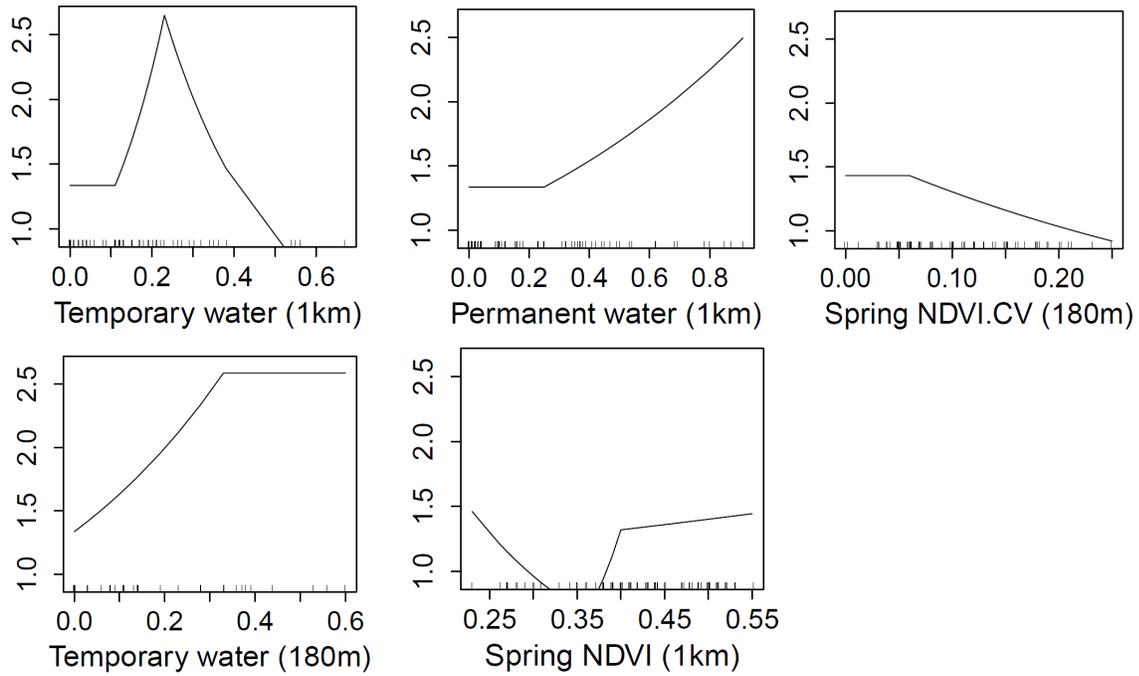


Figure 4.6. Habitat models for the log (y+1) mean relative abundance (y-axis) of the migratory least bittern (*Ixobrychus exilis*) within (a) fresh marsh and (b) intermediate marsh. Variables are in order of highest importance (left to right). The intermediate marsh model was developed from the inclusion of data from both marsh types. Rug plots show the distribution of x-axis data.

(a) Fresh marsh



(b) Intermediate marsh

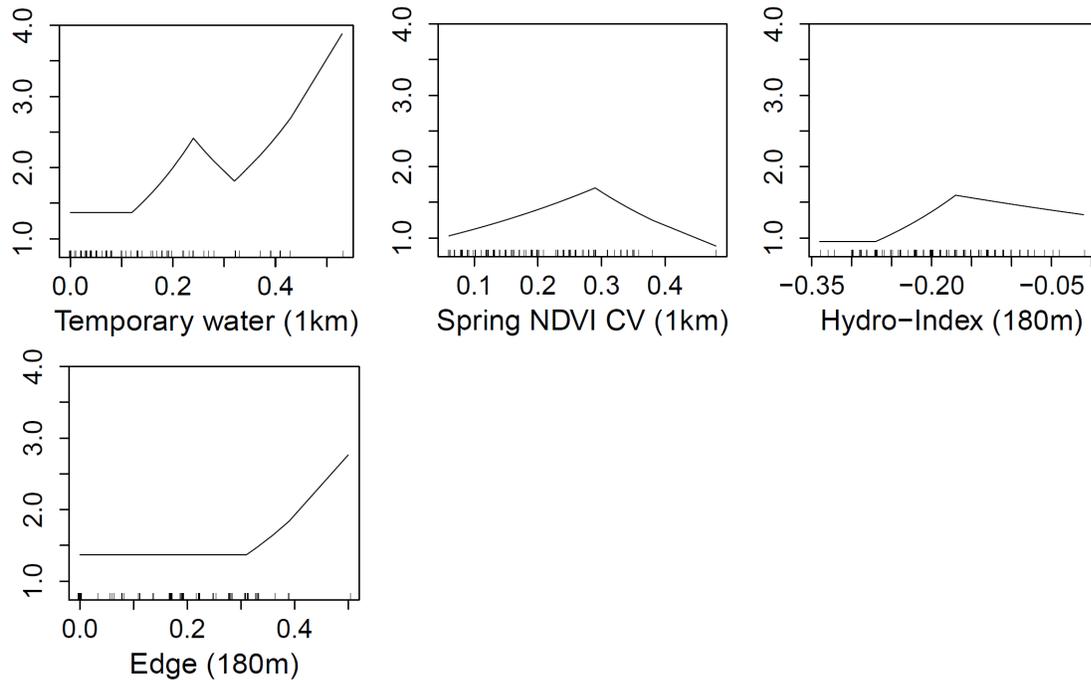


Figure 4.7. Habitat models for the log (y+1) mean relative abundance (y-axis) of the migratory purple gallinule (*Porphyrio martinica*) within (a) fresh marsh and (b) intermediate marsh. Variables are in order of highest importance (left to right). Rug plots show the distribution of x-axis data.

Temporal Transferability

The analysis of temporal transferability showed both migratory status ($F_{1,21}=6.48$, $p<0.05$) and marsh type ($F_{1,21}=18.58$, $p<0.001$) were predictors of temporal correlation among years. Predicted resident bird distribution was more spatially correlated over time compared to migratory birds, and spatial models in fresh marsh were less temporally correlated than those in intermediate marsh (Figure 4.8). The effect of marsh type was particularly large with all species in fresh marsh having a Spearman correlation of $R_s \leq 0.50$ among years. The two driest years, 2010 and 2011, were the most spatially correlated for all species. The mean predicted relative abundance of species did not explain variation in temporal correlation (linear regression, $t=0.49$, $p=0.61$, $n=24$). Regardless of the poor spatial correlation among years for birds in fresh marsh, purple gallinule, common gallinule, and least bittern maintained relatively constant predicted abundance over the entire region during my study (Figure 4.9). The result suggests a shift, but not a disappearance, of habitat for these species. The king rail predicted relative abundance in fresh marsh declined during the drought year of 2011. For intermediate marsh, mean predicted abundance declined for least bittern and purple gallinule during the drought year, but the other species remained relatively constant (Figure 4.9). My post-hoc analysis found temporary water was more common in fresh marsh and the variability in this marsh type was extreme within my study years (Figure 4.10). The variation in predicted relative abundance for the king rail and purple gallinule (Figures 4.11-4.14) are representative of species distributional changes in the two marsh types, and in some instances, clear changes took place due to the combination of weather, management activities, and disturbance (e.g. Figure 4.15). Additional habitat models are depicted in Appendix B.

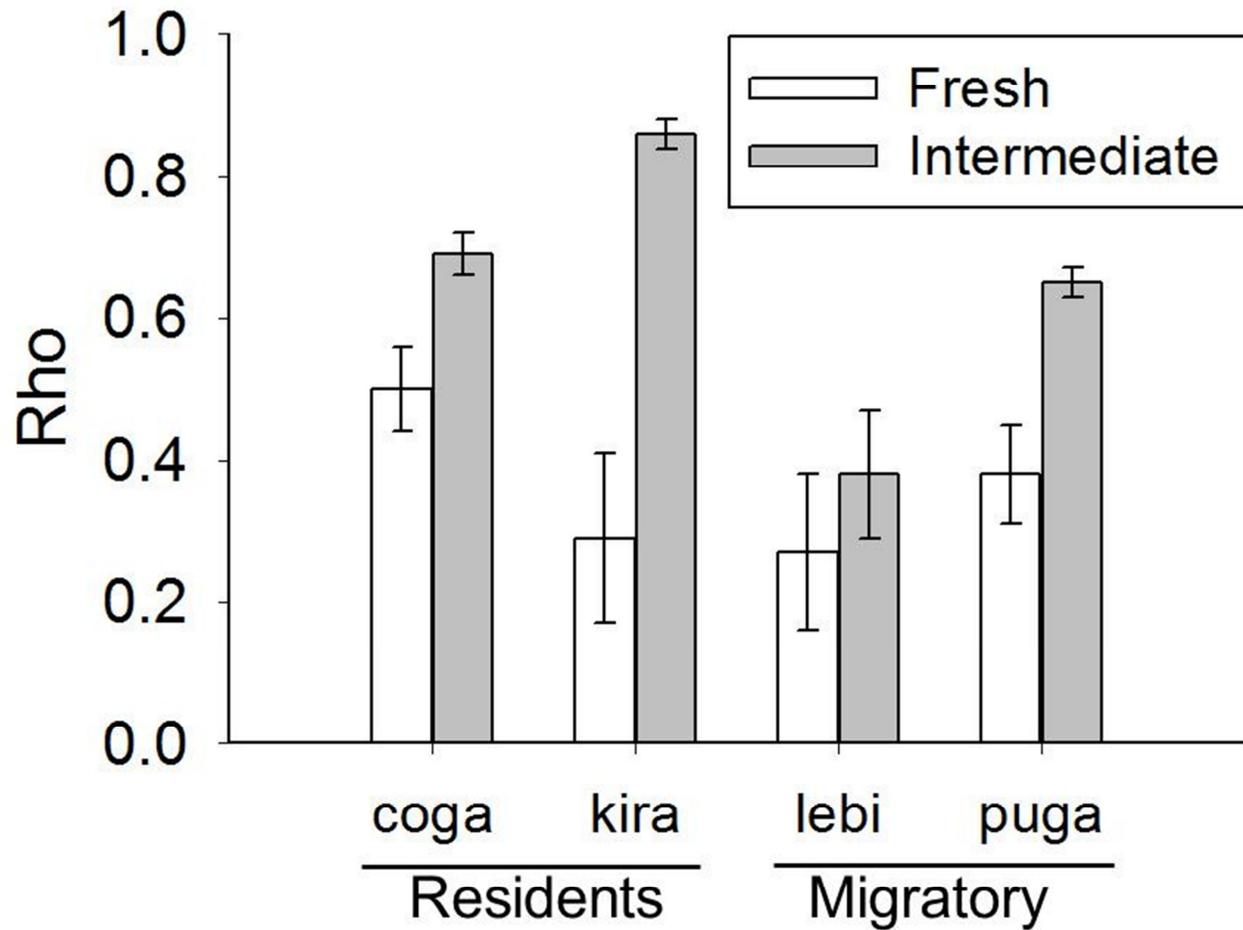


Figure 4.8. Mean temporal correlations of habitat models from 2009 to 2011 ($n=24$). coga=common gallinule, kira=king rail, lebi=least bittern, puga=purple gallinule. Models showed better annual correlation with resident breeding birds and within intermediate marsh. The mean is reported with $\pm 1SE$.

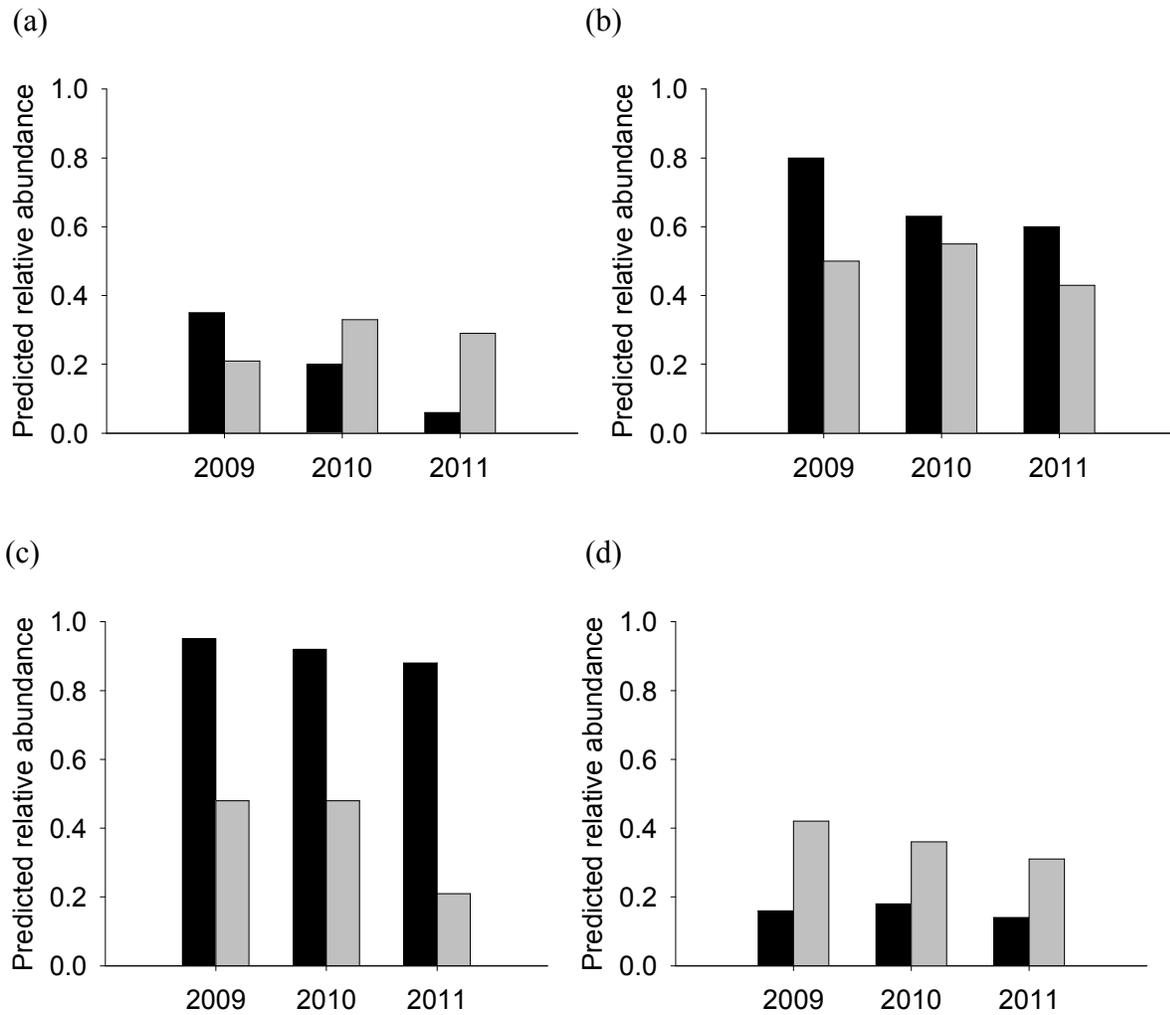


Figure 4.9. Mean relative abundance of birds by year for the entire region of fresh marsh in southwest Louisiana (91,762 100m² cells) and the intermediate marsh in Texas (63,209 100m² cells), The resident breeding birds: (a) king rail, (b) common gallinule, and migratory breeding birds: (c) least bittern, and (d) purple gallinule. Black bars represent fresh marsh and gray bars are intermediate marsh. SE is not given because the entire survey area was calculated.

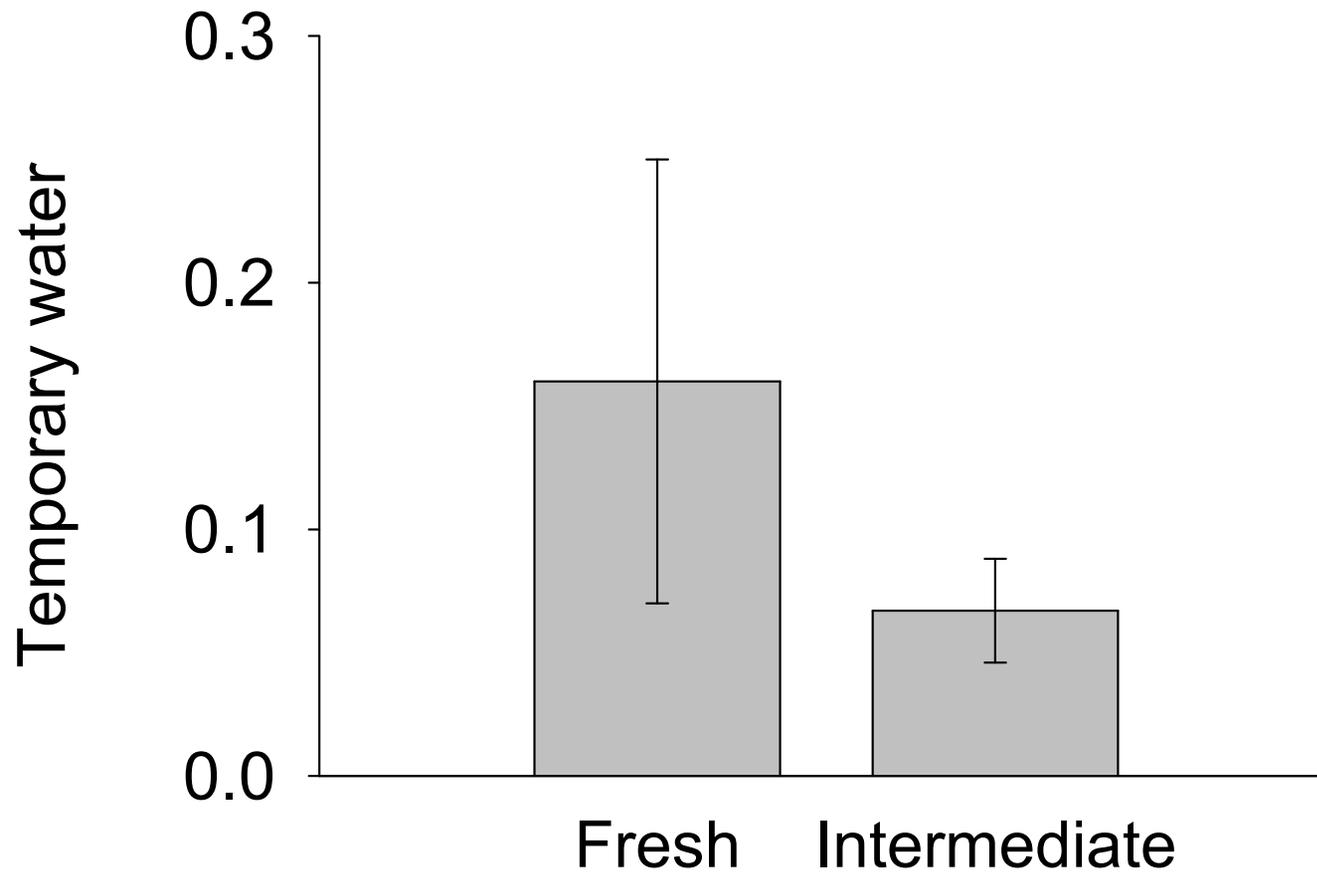


Figure 4.10. The proportion of area with temporary water per 1000 m² for the three study years (2009-2011, $n=3$). Fresh marsh included all fresh marsh in southwestern Louisiana, and intermediate marsh included the Texas study area extent east of McFaddin National Wildlife Refuge. The mean is reported with $\pm 1SE$.

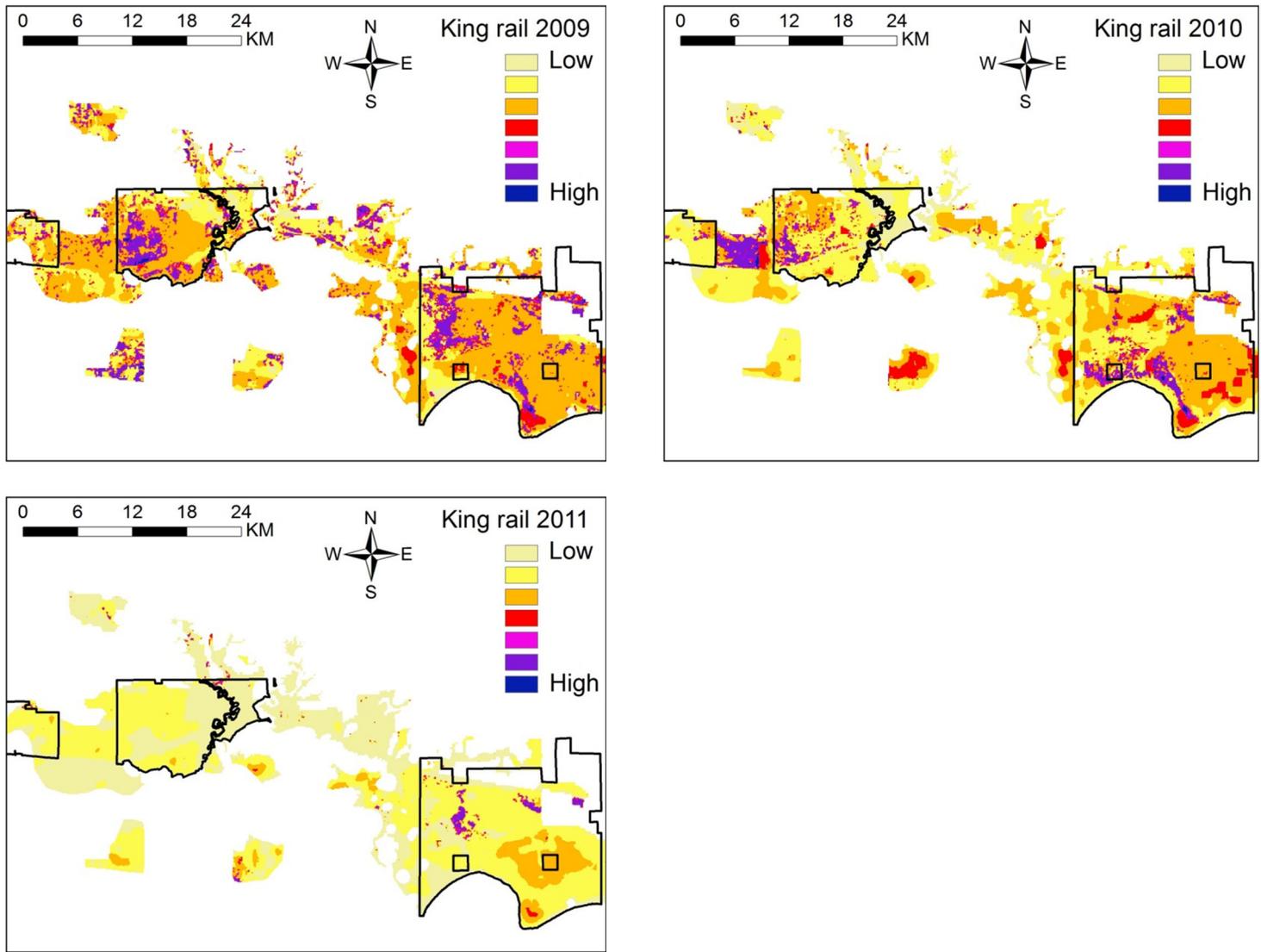


Figure 4.11. King rail (*Rallus elegans*) predicted relative abundance in fresh marsh 2009-2011.

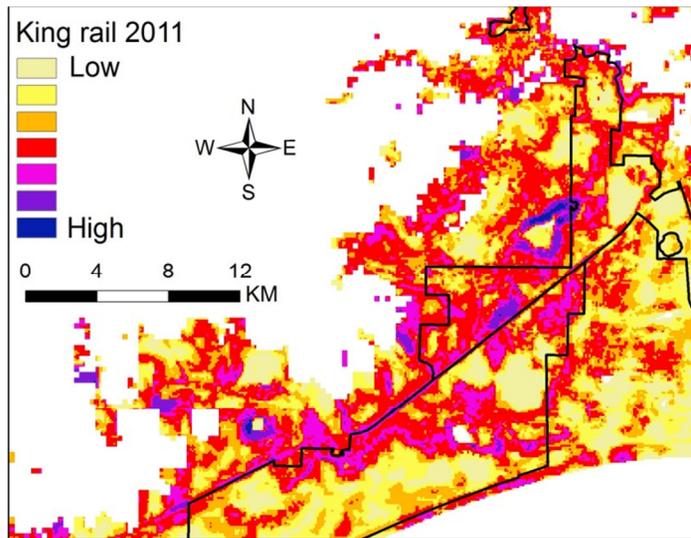
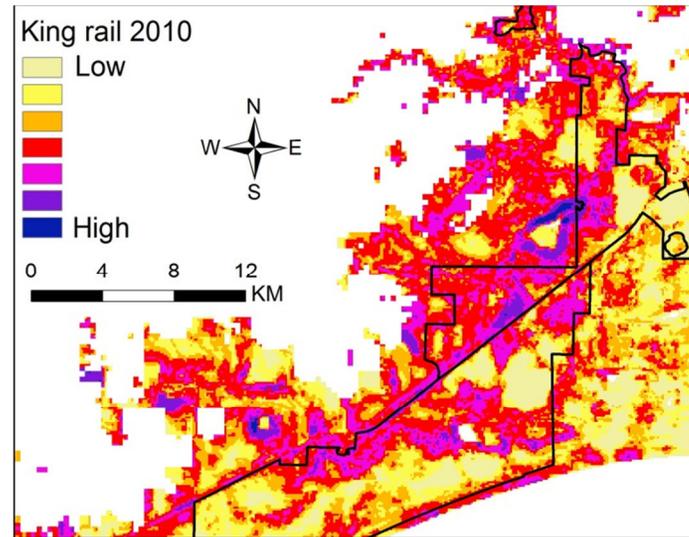
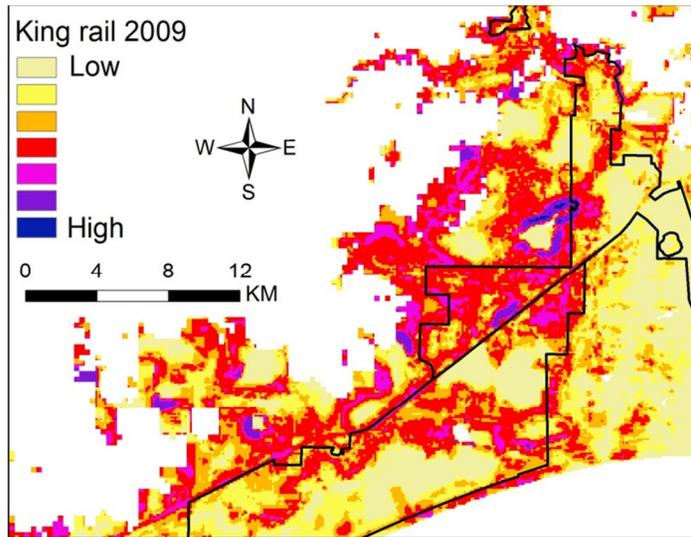


Figure 4.12. King rail (*Rallus elegans*) predicted relative abundance in intermediate marsh 2009-2011.

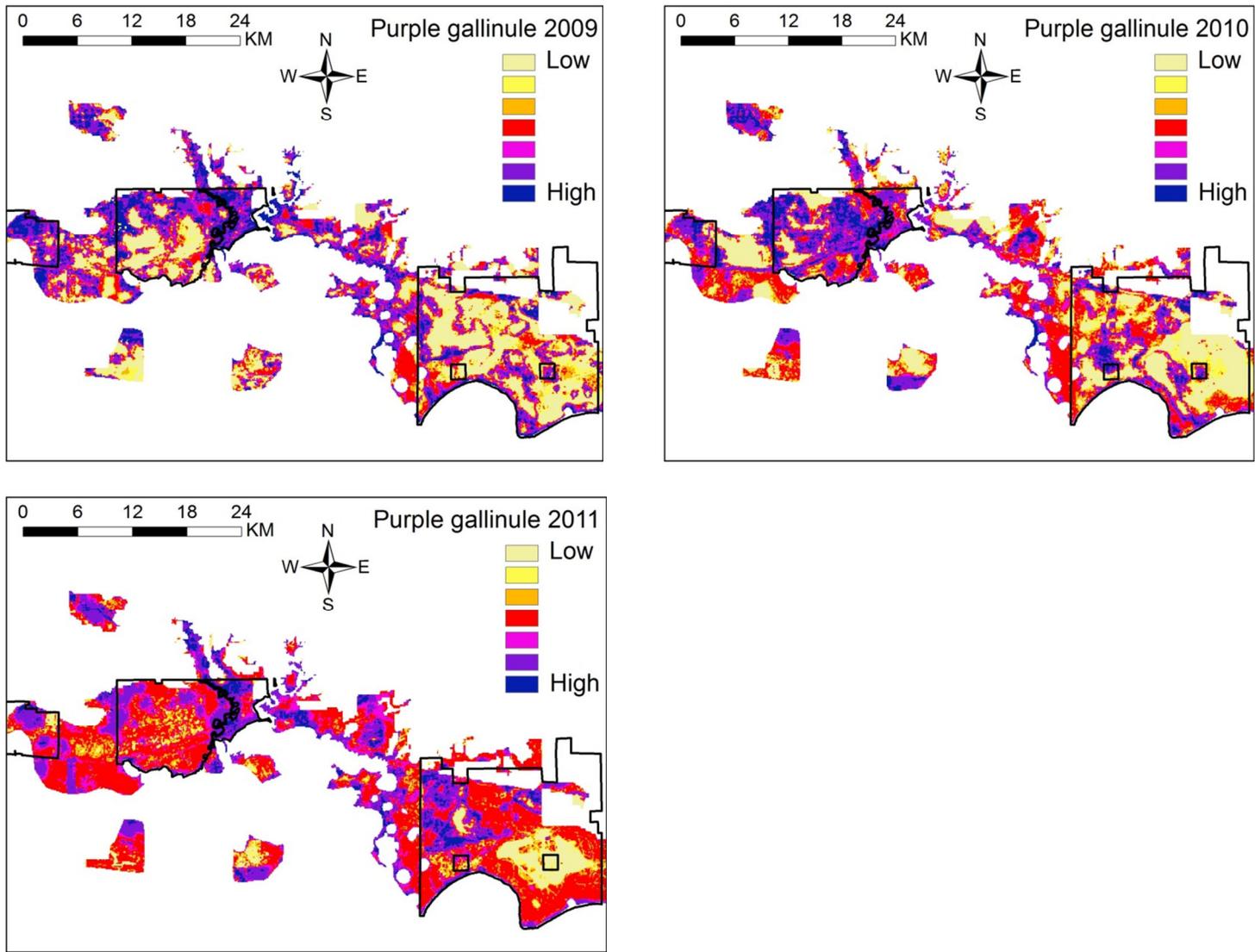


Figure 4.13. Purple gallinule (*Porphyrio martinica*) predicted relative abundance in fresh marsh 2009-2011.

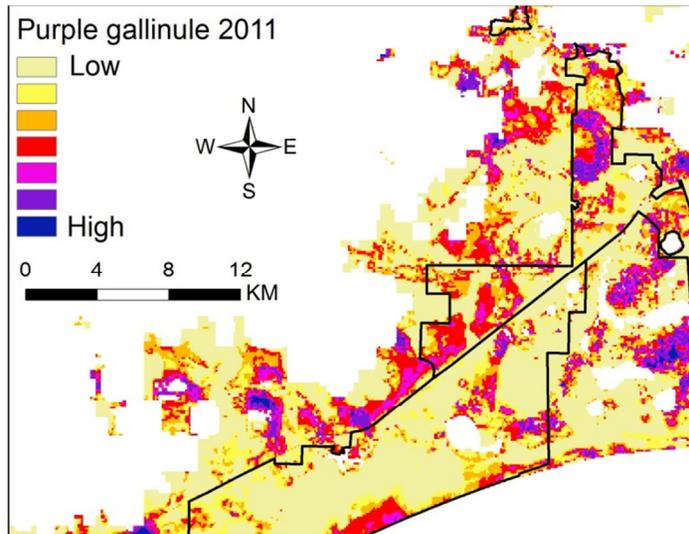
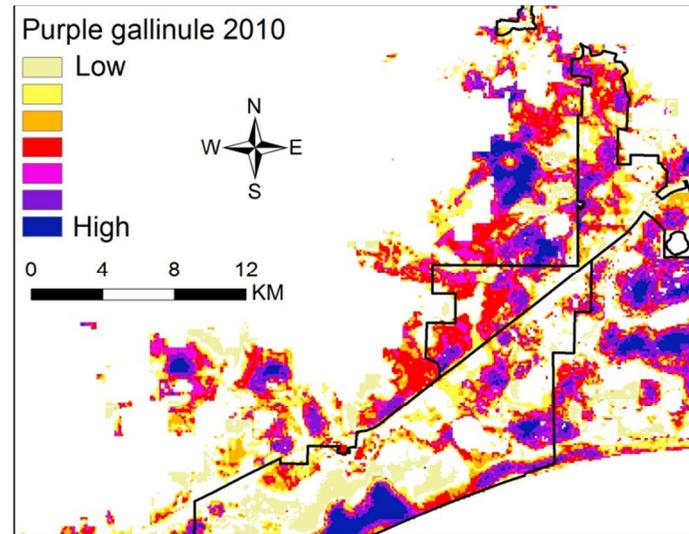
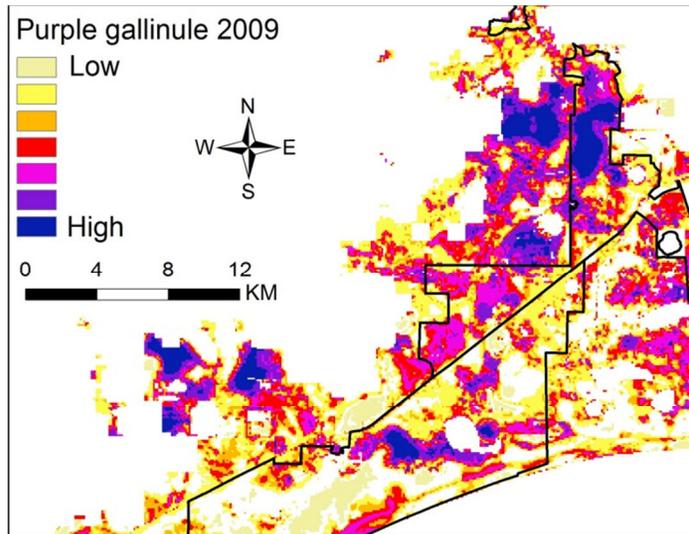


Figure 4.14. Purple gallinule (*Porphyrio martinica*) predicted relative abundance in intermediate marsh 2009-2011.

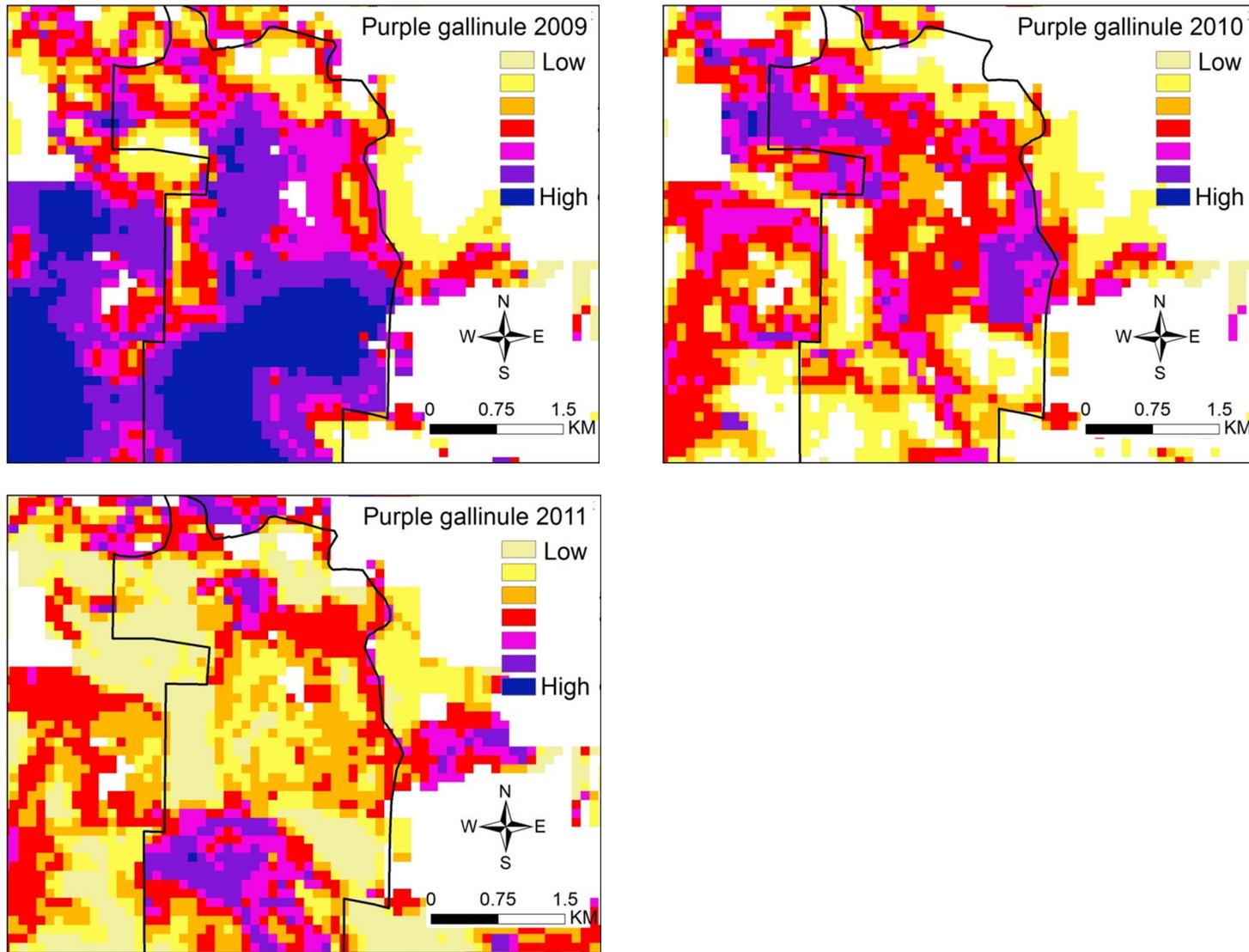


Figure 4.15. The effect of management and weather on purple gallinule (*Porphyrio martinica*) predicted relative abundance at several impoundments within JD Murphree WMA, Texas (black outline). In 2009, water was held on the marsh longer than typical, 2010 was a typical drawdown year, and 2011 was a drought year.

DISCUSSION

I used satellite remote sensing to procure wetland-related habitat variables that were directly related to marsh bird ecology over space and time. My hypothesis of spatial transferability between marsh types was rejected because I found models developed for a specific marsh type were poor predictors of birds in the other marsh type. Likewise, marsh-specific models of bird distribution were usually better predictors of relative bird abundance compared to predictions from a single, general model. Overall, the spatial transferability and model generality results revealed the bird-habitat relationship was not consistent across fresh and intermediate marshes. For the tests of temporal transferability, I hypothesized that the distribution of resident birds would be more correlated among years compared to the migratory species. The results supported this hypothesis, but marsh type was also a strong predictor of temporal transferability. Specifically, the predicted distribution of birds in fresh marsh was poorly correlated among years compared to birds in intermediate marsh. This result appeared to be a function of birds in fresh marsh being more closely related to habitat features that were spatially variable among years. Birds in intermediate marsh were more strongly related to long-term characteristics of wetland habitat.

While research has linked spatial and temporal precipitation patterns to wetland bird distribution (Forcey et al. 2011), I have developed spatial variables and indices that directly link birds to specific habitat components and wetland processes. My results demonstrate the capability of satellite remote sensing to quantify biological processes based on multi-temporal imagery. Similar to land cover change studies, previous use of multi-temporal satellite data in wetlands has emphasized classification categories to quantify wetland loss (Allen et al. 2012) and changes in vegetation composition (Klemas 2011). Here, I was able to distinguish fine-scale

attributes, such as temporary and permanent open water and the heterogeneity of wetness over space and time. Due to the low elevation gradient and widespread human-modifications to wetland systems, flooding regimes are inherently difficult to quantify. Yet, the hydroperiod of wetlands has been linked to the abundance and composition of wildlife, fish, and macroinvertebrates (Brooks 2000, Snodgrass et al. 2000, Van Buskirk 2005). The importance of wetland hydroperiod was reinforced by my results because temporary water, permanent water, and the long-term hydro-indices were common factors in models; these multi-temporal variables were 50% (16 of 32) of the total variables selected. Therefore, the use of multi-temporal imagery could play a major role in developing models for a variety of taxa in wetland ecosystems. Generally, indices have an advantage over classified satellite imagery because ground-truthing is minimized (Lahoz-Monfort et al. 2010), and yet broad biophysical properties can be interpreted (e.g. Mueller et al. 2008). In this study, many variables were dependent on Landsat band 5, which is readily absorbed by water. The usefulness of Band 5, and indices derived from it, builds upon previous studies using NDVI and its heterogeneity to model the distribution of species (Aldridge and Boyce 2007, Bellis et al. 2008), and I suggest much more diverse indices could be developed for SDMs.

My results from satellite remote sensing are consistent with, and expand upon, knowledge of species ecology. For king rails in intermediate marsh, my field study showed a strong negative relationship with drawdown marsh management (Chapter 3). Correspondingly, remote sensing results indicated a negative correlation with the heterogeneity of wetness over time, and this was the second most important variable in the model. In contrast, king rails in fresh marsh were positively related to drawdown management in the field study, but the corresponding variable was not included in the remote sensing model. Nonetheless, temporary

water was the most important factor, and temporary water in the late spring was often the result of a slow drawdown of water. Open water-vegetation edge is known as a habitat preference for most secretive marsh birds (Lor and Malecki 2006, Rehm and Baldassarre 2007), and the edge variable was one of the most common variables in my study. Additionally, the results reveal several new findings in secretive marsh bird ecology. In particular, the selection of temporary or permanent water likely reflects water depth, food availability, and the hydroperiod of the area. Common gallinule abundance has been positively related to water depth (Tozer et al. 2010) (Chapter 3), and the positive correlation with permanent water probably signifies this relationship. In contrast, king rails responded to temporary water and spatial heterogeneity in wetness, which likely related to their use of shallow water and small pools of water, respectively. My study also revealed the importance of short- and long-term wetness, as well as the spatial heterogeneity of wetness for many species.

Overall, the spatial transferability of models between fresh and intermediate marsh types was poor even though previous research on marsh birds identified only a few predictors related to marsh bird distribution (e.g. edge, water depth). Similarly, general models resulted in a lower predictive ability compared to marsh-specific models. This result is consistent with the trade-off of model generality and precision (Fielding and Haworth 1995), and the spatial scale of inference is also important. Certainly, combining both marsh types explained additional variance due to species' abundance differences between fresh and intermediate marshes. However, the lower precision within each marsh type raises the question, when do we clump or split habitat types for SDMs? Studies of sample size requirements in SDMs show from 50 to 100 samples maximize performance (Stockwell and Peterson 2002, Kadmon et al. 2003, Hernandez et al. 2006), and this may be taken as a minimum requirement. Other considerations include the range of abiotic

predictors (Randin et al. 2006), changes in biotic factors (Gray et al. 2009), directness of predictor variables to species (Vanreusel et al. 2007), and differences in dominant landscape features (Zharikov et al. 2007).

One potential issue with satellite-derived variables is that changes in vegetation composition may cause differences in the species-environment relationship. For example, the threshold spring NDVI for king rails in intermediate marsh corresponded with large areas of unbroken marsh dominated by *Spartina patens* (Figure 4.2). In fresh marsh, *S. patens* were uncommon, and the negative association with spring NDVI had a different threshold and a more gradual slope. The wetness indices I developed may also be influenced by vegetation composition and its characteristics, such as senescence and phenology. Therefore, transferability of models developed from remote sensing indices may transfer to different regions if the vegetation composition remained constant, or with fine-tuning of species-environment relationships, given a set of predictor variables. Further research is needed with the transferability of indices derived from remote sensing.

I hypothesized that open water and edge variables would directly relate to marsh birds regardless of marsh type, and the use of indices should not affect these results. Another potential issue with spatial transferability is the truncation of predictor variables within a particular region, or habitat, compared to the full environmental range experienced by a species (Randin et al. 2006). For example, the transferability of marbled murrelet (*Brachyramphus marmoratus*) models showed success in only 50% of cases because bird presence at some sites was driven by anthropogenic fragmentation, but other sites did not show extensive fragmentation (Zharikov et al. 2007). I discarded the possibility of truncated variables because my training dataset was very similar in both marsh types (Table 4.2). The one exception was the lower winter NDVI observed

in fresh marsh, which was likely why the variable was a predictor of king rails in fresh marsh, but not intermediate marsh.

In my study, the primary determinant of poor transferability between marsh types was the differing response of birds to habitat variables. Birds in intermediate marsh selected for long-term variables, such as the hydro-index, while fresh marsh models were characterized by more short-term, snapshot variables. Correspondingly, my post-hoc analysis showed temporary water was more common in fresh marsh and its variability was more extreme than intermediate marsh during the course of my study. Therefore, regional variation may occur because birds in fresh marsh were selecting for temporary water, which was not as common in intermediate marshes. Birds in intermediate marsh largely selected for long-term wetter conditions and heterogeneity, which may be more predictable on an annual basis. This result contrasts with studies showing similar predictor variables and parameter estimates for transferred habitat models (Whittingham et al. 2007, Gray et al. 2009), and my study presents evidence that habitat selection is context dependent, as suggested by Whittingham (2007).

To my knowledge, no previous studies have used a spatial model to quantify changes in the annual spatial distribution of migratory or resident birds. While non-spatial population studies have addressed factors such as weather (Cormont et al. 2011) and disturbance (Bechtoldt and Stouffer 2005), spatial modeling has rarely addressed these short-term dynamics. The species analyzed here are limited in number, but the poor temporal correlations I observed merits further research, especially with migratory birds in dynamic ecosystems. Invasive species have been recognized as being in non-equilibrium with their environment (Elith et al. 2010, Vaclavik and Meentemeyer 2012), but other species have not been widely recognized as having a dynamic distribution over time. Migratory birds have been shown to be more correlated with broad-scale

landscape features, such as fragmentation, compared to resident birds (Flather and Sauer 1996, Mitchell et al. 2001). However, it is unclear if the migratory bird response is due to their increased mobility, and therefore, increased response rate to landscape change (e.g. fragmentation) or due to other ecological factors. A rapid response of migratory birds was demonstrated by Jones et al. (2003), who found neotropical migratory birds exhibited more synchronous abundance compared to short-distance migrants and resident species in boreal forests, and the underlying factor was likely food abundance. In wetlands, the migratory yellow-headed blackbird (*Xanthocephalus xanthocephalus*) responded to drought with both a lower density of birds and total reproductive failure (Fletcher and Koford 2004). Some research has been devoted to species traits related to SDM success (e.g. McPherson and Jetz 2007), but an investigation into ecosystem traits would be beneficial. In my study, the predicted spatial distribution of birds varied considerably among years, and the difference was more extreme in fresh marsh compared to intermediate marsh.

Marsh is a dynamic ecosystem with temporal changes due to rainfall, drought-wildfire relationships, and anthropogenic factors (Han et al. 2007). I found birds in fresh marsh were selecting for the more dominant feature on the landscape, temporary water, and this ephemeral habitat had a high variability on an annual basis. Additionally, the edge of temporary water (~30% temporary water) was the most important variable for the two gallinule species in fresh marsh, and this edge habitat is a function of annual rainfall and the rate of water recession during the late spring. The higher quantity and variability in temporary water within fresh marshes suggests that birds, particularly migratory birds, could benefit from an ability to track these resources over time. The relatively poor temporal transferability of fresh marsh birds suggests ecosystems prone to disturbance events, or with dependence on annual rainfall (e.g. grasslands,

wetlands, savannas, forests with insect outbreaks), may have species with poor temporal transferability. For example, Pickens and King (2012) found a king rail model over-predicted bird occurrence, and suggested that the available spatial data was not representative of the most recent temporal changes in succession and spread of an invasive species. Albright et al. (2010) documented sizeable decreases in bird abundance throughout the central United States due to precipitation and drought conditions. They found neotropical migratory bird abundance and richness were most negatively affected by drought, short-distance migrants were mildly affected, and residents actually had a positive response. Therefore, conservation planning and management needs to incorporate the distribution of species over multiple years representative of disturbance regimes and weather conditions.

Recent research has shown land cover improves climate-based SDMs (Venier et al. 2004, Tingley and Herman 2009), and I have further demonstrated that a finer spatial and temporal resolution of habitat can result in SDMs with good predictive ability within land cover types, such as wetlands. Land cover may be considered static over relatively long time frames, but indices, like the ones I have used, may be less powerful outside the temporal scale of sampling. For instance, a study of the giant panda (*Ailuropoda melanoleuca*) found the mean NDVI over several years provided better predictions compared to single-year NDVI (Tuanmu et al. 2011). They emphasized the method used to create remote sensing variables will have substantial effects on the temporal transferability of models. In contrast to the largely sedentary giant panda, my study shows birds selected habitat that changed annually in fresh marsh. In intermediate marsh, long-term abiotic factors played a larger role, and models were more spatially stable over time. The year-specific models may be useful for monitoring species over short and long time series. While most monitoring programs survey localized areas (U.S. Breeding Bird Survey) over

years, the examination of the entire region via remote sensing can give a more regional approach to monitoring. In addition, temporal heterogeneity revealed in remote sensing may explain inter-annual species trends, and clarify long-term trends. While migratory birds may simply move to new areas with changing habitat conditions, the response of resident birds is unclear. The NDVI have been linked to the survivorship of birds (Schaub et al. 2005, Grande et al. 2009, Wilson et al. 2011) and this is one possibility. In the drought year of my study (2011), king rails were difficult to locate in fresh marsh, while intermediate marsh rails had higher mortality and lower reproductive success (Chapter 2). With the recent interest in habitat monitoring over large spatial scales (see review by Lengyel et al. 2008, Singh et al. 2010), the capability of satellite data in modeling species and habitat condition should be further explored.

In conclusion, the use of novel satellite remote sensing techniques in distribution models is a rapidly growing area of research (Franklin 2009, Cord and Rodder 2011), and such research could lead to a better understanding of species' distribution over space and time. In the future, satellite data will likely increase the spatial extent of habitat studies, while simultaneously examining a finer spatial and temporal resolution. While the sample size available for modeling increases with the development of a single model, splitting the data into different categories of habitat can increase the predictive power of the models. My temporal transferability results caution the interpretation of SDMs relating long-term survey (or museum) data to environmental variables that are a single snapshot in time (e.g. climate, landcover). For example, research could show a trend with climate, which is actually a result of short-term population oscillations, disturbance events, or weather. In these cases, a solution may include accounting for short-term variation as much as possible.

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CHAPTER 5: GENERAL CONCLUSIONS

A multi-scale perspective is essential in species' ecology (Wiens 1989), and here, I have used traditional wildlife field data combined with satellite remote sensing to gain new insights into marsh bird ecology. While predictive modeling can sometimes provide little inference, here I have shown species distribution models derived from satellite remote sensing reflected data collected on-the-ground. Furthermore, new variables, such as heterogeneity of vegetation and wetness over a 1000 m² area were demonstrated to be important for marsh birds. Open water, and its associated edge, is usually measured in marsh bird studies, but remote sensing allowed me to distinguish between temporary and permanent open water. In fact, remote sensing models (Chapter 4) explained more variation in relative bird abundance than the field-based models (Chapter 3). From the microhabitat scale, king rails (*Rallus elgans*) often selected small ponds near thick vegetation, and correspondingly, the remote sensing results showed wetness heterogeneity and open water were important components of king rail habitat in intermediate marsh. In Chapter 3, I found a positive association between king rails and drawdowns in fresh marsh, and the remote sensing results showed a similar relationship via a positive correlation with temporary water in the late spring. This temporary water was often the result of water being held on the marsh, and then ponds formed while the marsh was being slowly drained. Overall, the spatially explicit modeling assisted to examine broad-scale patterns, and reemphasized the results of Chapter 3 that showed broad marsh types and management affected bird prevalence. Fundamentally, the broad context of wetland habitat affects marsh birds beyond the typical 100 m of bird survey areas.

In addition to the spatial component of my study, I had several results associated with the temporal aspects of the bird-environment relationship. The effect of the 2011 drought was

quantified by a decrease in adult survivorship from 90% to 60% for the breeding season. Plus, king rail chicks and juveniles were largely absent in the drought year. Complementing these data, the remote sensing research showed dramatic decreases in the predicted distribution of the king rail in fresh marsh. Other species, such as the purple gallinule (*Porphyrio martinica*), also showed changes in distribution due to a combination of management and weather.

Future research should investigate the use of satellite remote sensing to monitor populations at broad spatial scales. Complex modeling procedures may need to be simplified with the objective of efficiently modeling at a regional scale, and the identification of indicator species could be beneficial. Feng et al. (2010) reviews the use of remote sensing for assessing ecosystem services, and they note ecologists often lack the skills to do broad-scale studies, while remote sensing experts generally do not focus on ecological questions. However, in Europe, monitoring efforts have used satellite remote sensing to identify how land use changes are predicted to effect ecosystem services, including crop production, wildlife products, habitat diversity, and recreation (Haines-Young et al. 2012). Nonetheless, the use of satellite remote sensing is only beginning to be used for species distribution modeling (Franklin 2009), and further developments are likely to be made in the coming decades.

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APPENDIX A

Landsat Images Obtained:

Seasonal Categories: Winter- Nov 1-Feb 28, Spring- Mar 1-June 30, Summer- July 1-Oct.31

Louisiana:

Winter=

Feb 12, 2006
Feb 18, 2008
Dec 2, 2008
Feb 20, 2009
Dec 5, 2009
Jan. 22, 2010
Dec. 24, 2010

Spring=

8) Mar 5, 2008
9) June 28, 2009- No hydro-index (some clouds)
10) April 28, 2010
11) May 17, 2011

Summer=

12) July 27, 2008
13) Oct 31, 2008
14) Oct. 18, 2009
15) August 2, 2010
16) Oct. 5, 2010
17) Sept. 6, 2011

Texas:

Winter=

Jan 18, 2006
Dec 4, 2006
Feb. 6, 2007
Feb 9, 2008
Nov 26, 2009
Feb 11, 2009

Spring=

April 8, 2006
March 12, 2008
April 29, 2008
May 18, 2009

March 18, 2010
May 5, 2010

Summer=
Oct. 17, 2006
Sept 4, 2008
Oct 25, 2009
Aug 25, 2010

APPENDIX B

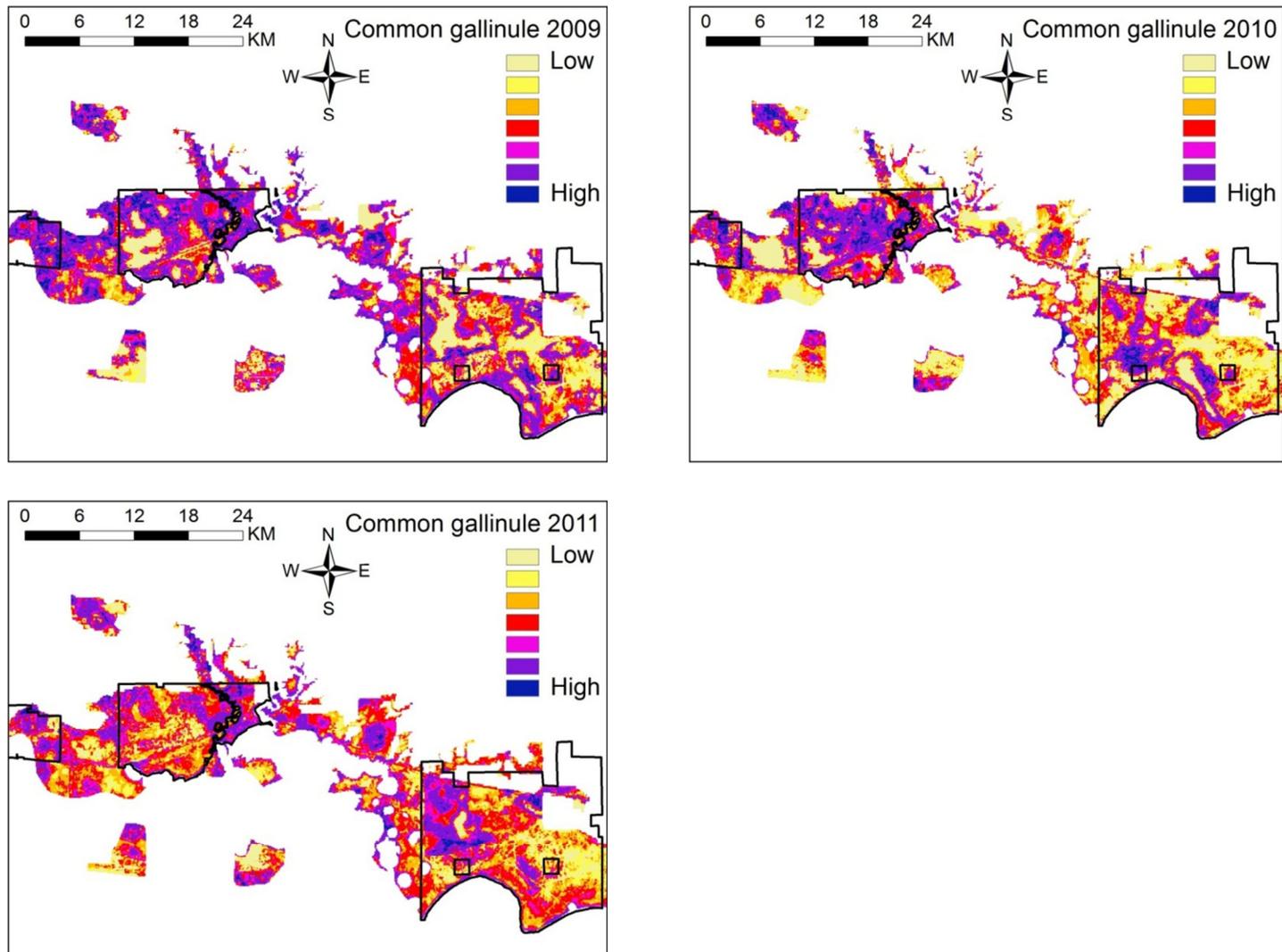


Figure B.1. Common gallinule (*Gallinula galeata*) predicted relative abundance in fresh marsh 2009-2011.

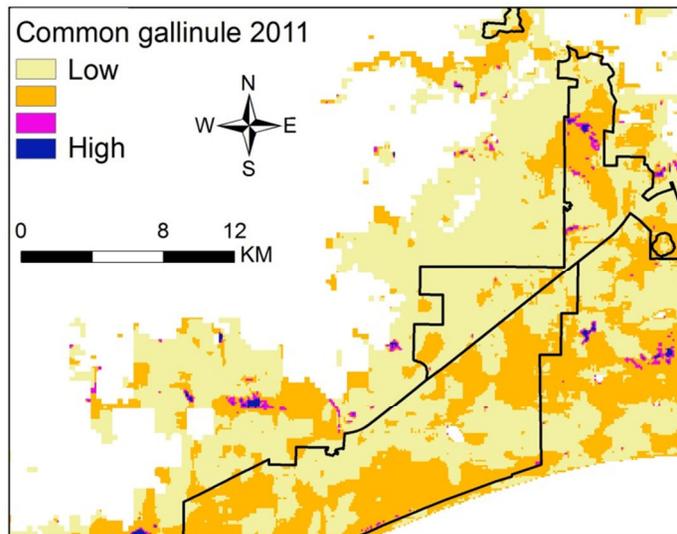
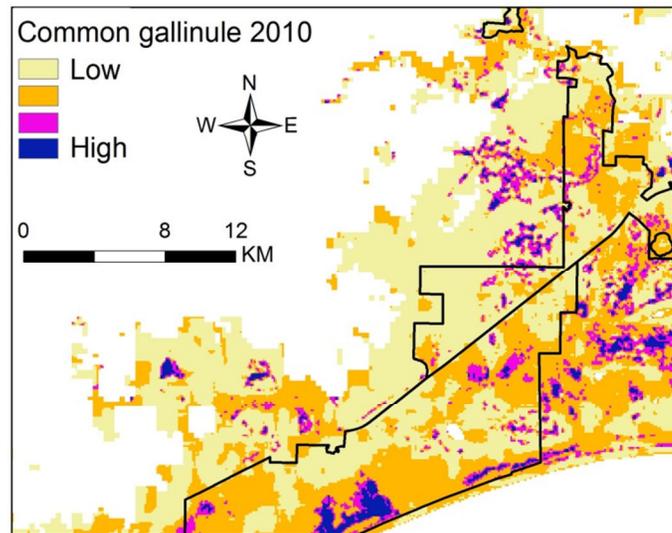
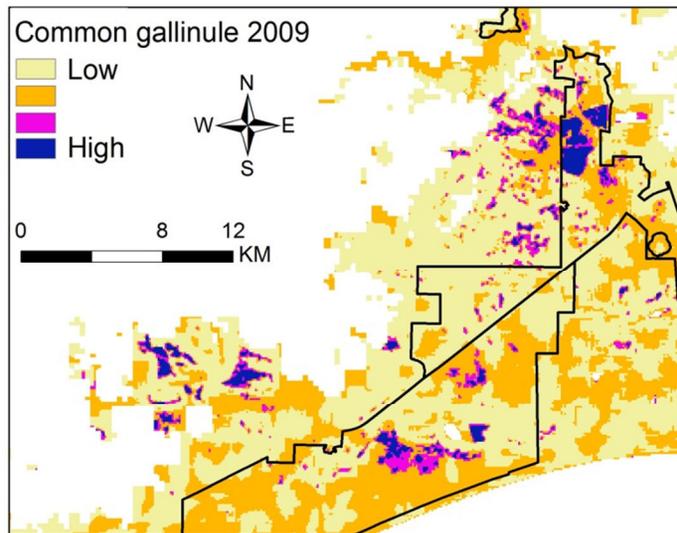


Figure B.2. Common gallinule (*Gallinula galeata*) predicted relative abundance in Texas intermediate marsh 2009-2011.

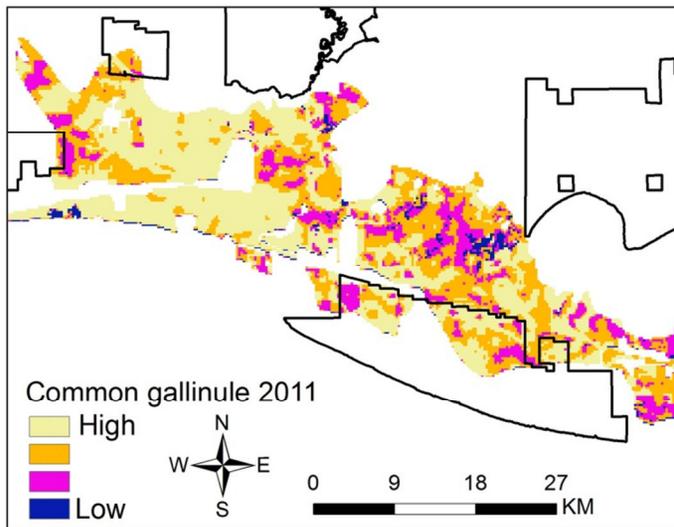
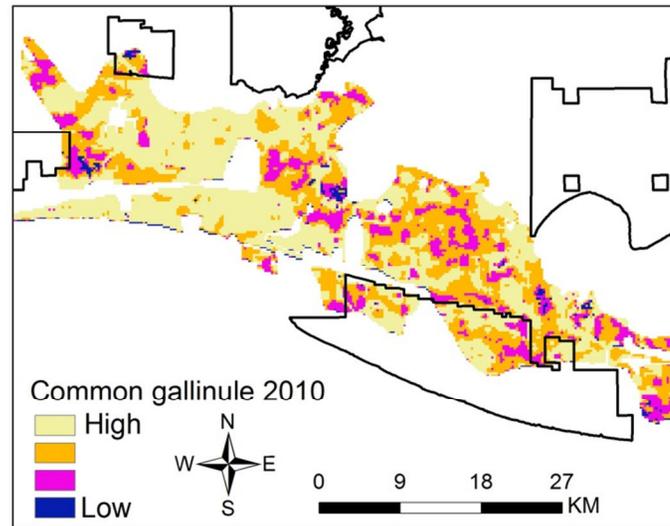
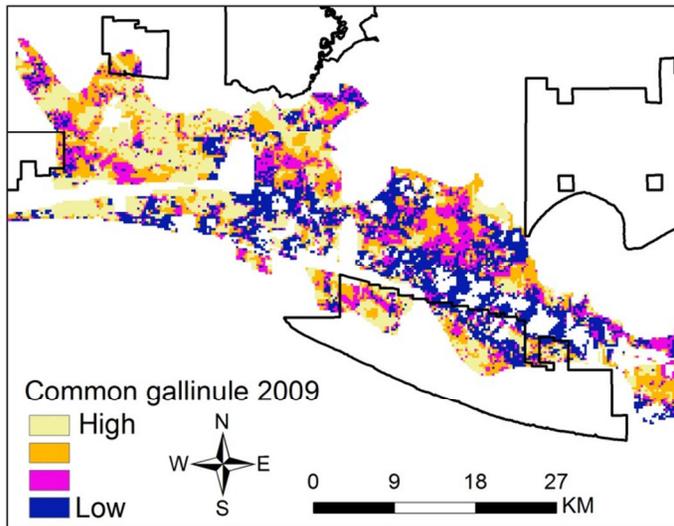


Figure B.3. Common gallinule (*Rallus elegans*) predicted relative abundance in Louisiana intermediate marsh 2009-2011.

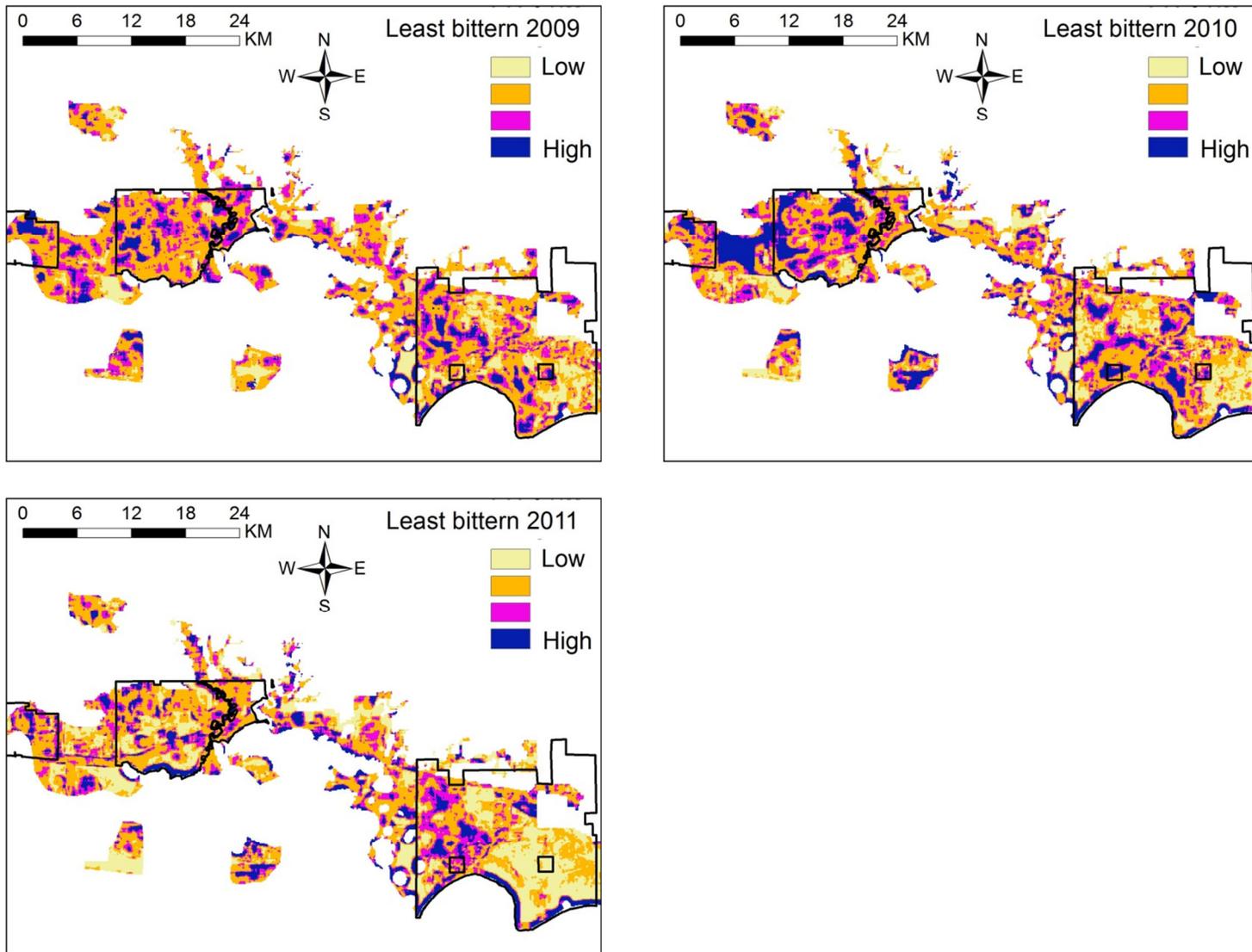


Figure B.4. Least bittern (*Ixobrychus exilis*) predicted relative abundance in fresh marsh 2009-2011.

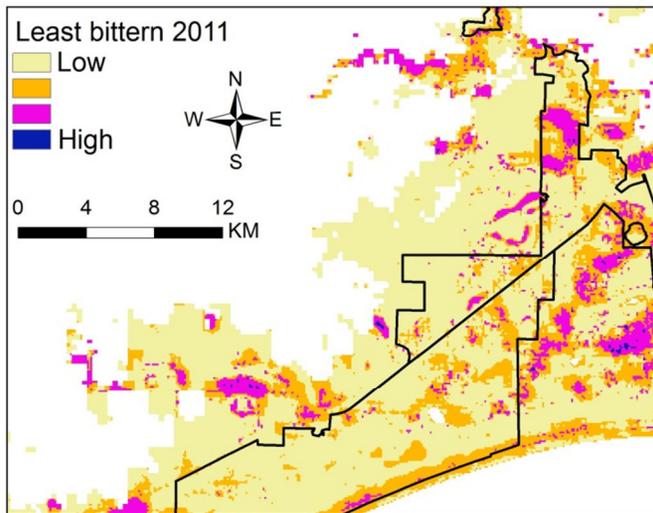
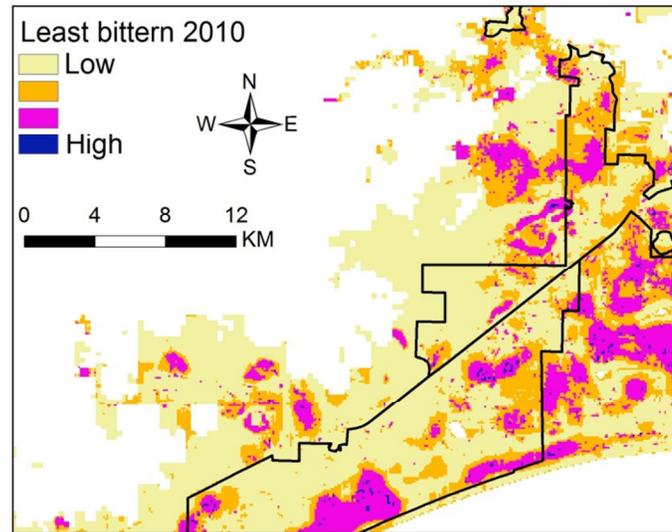
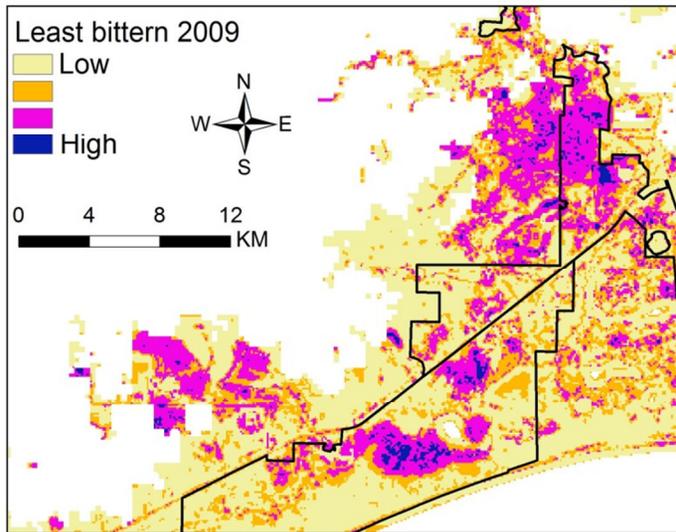


Figure B.5. Least bittern (*Ixobrychus exilis*) predicted relative abundance in Texas intermediate marsh 2009-2011.

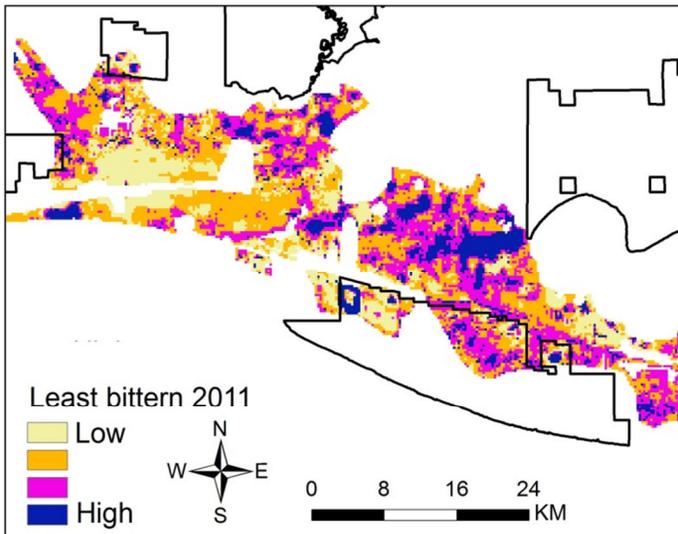
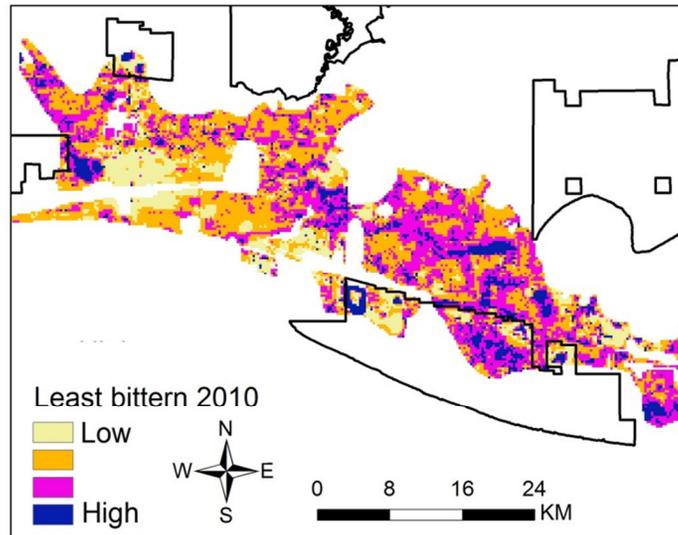
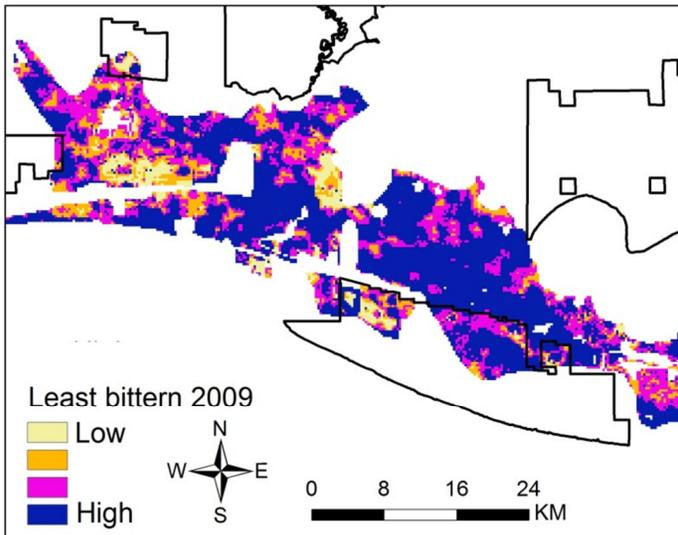


Figure B.6. Least bittern (*Ixobrychus exilis*) predicted relative abundance in Louisiana intermediate marsh 2009-2011.

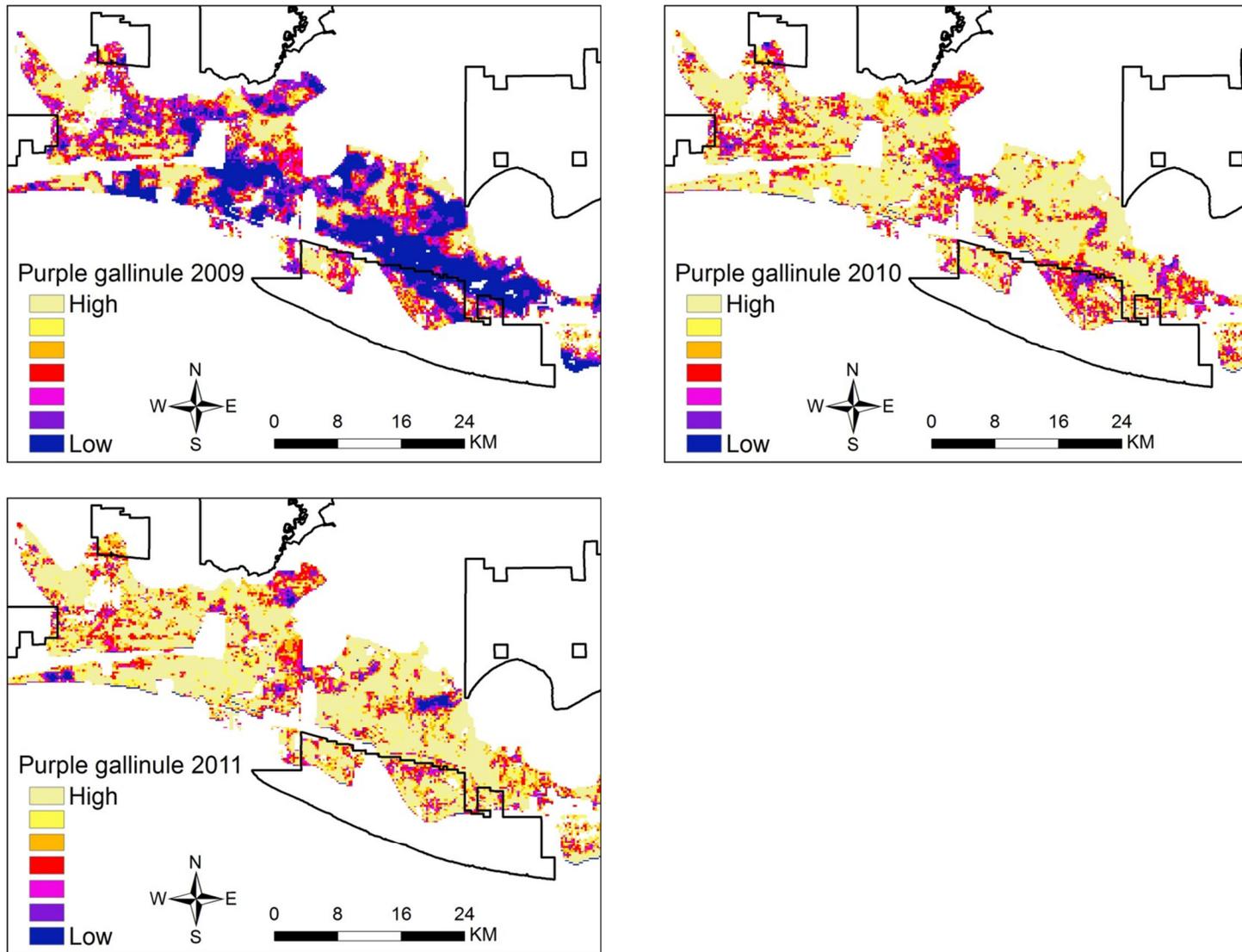


Figure B.7. Purple gallinule predicted relative abundance in Louisiana intermediate marsh 2009-2011.

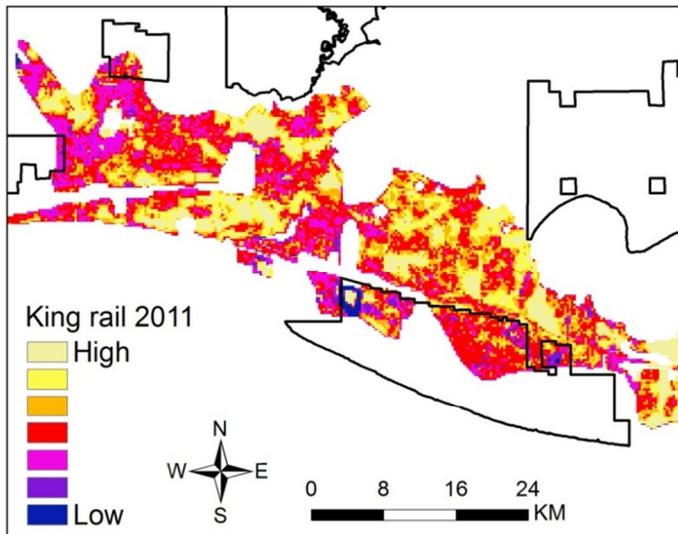
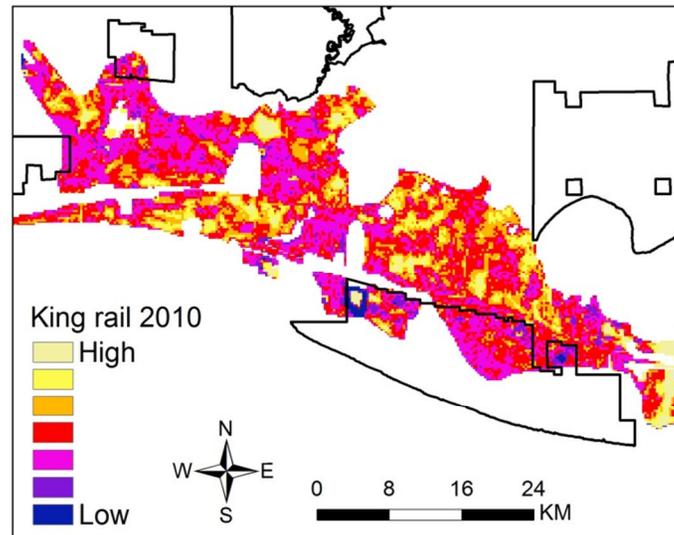
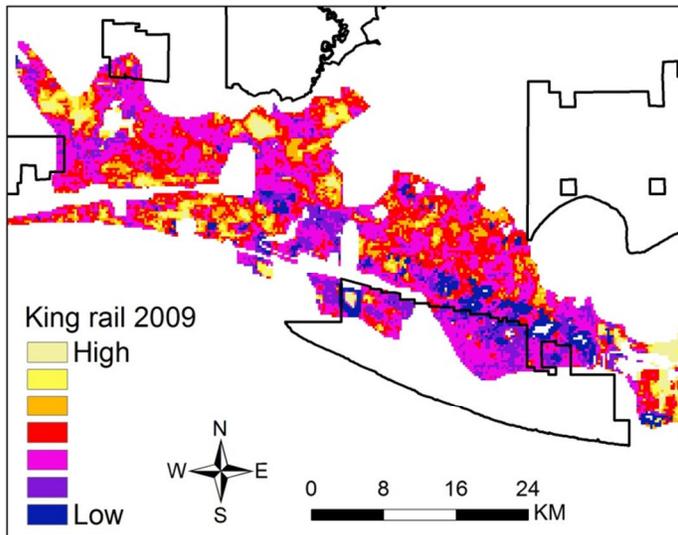


Figure B.8. King rail (*Rallus elegans*) predicted relative abundance in Louisiana intermediate marsh 2009-2011.

VITA

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