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Assessing the Vulnerability of Coastal Marsh Birds to Sea Level Rise in the South Atlantic Coast

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ASSESSING THE VULNERABILITY OF COASTAL MARSH BIRDS TO SEA
LEVEL RISE IN THE SOUTH ATLANTIC COAST

A Thesis
Presented to
the Graduate School of
Clemson University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science
Wildlife and Fisheries Biology

by
Nicolette Roach
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Accepted by:
Dr. Kyle Barrett, Committee Chair
Dr. Patrick Jodice
Dr. Yoichiro Kanno

ABSTRACT

Global wetland degradation and loss is occurring at a rapid rate, and in the United States over 50% of wetlands in the lower 48 states have been altered since European settlement. In some cases, wetlands that were historically transformed for agriculture are now managed as wetland habitat. We conducted occupancy surveys for black rails (*Latterallus jamaicensis*) in managed and unmanaged areas of coastal South Carolina. We modeled landscape and local factors potentially influencing occupancy and we assessed whether these habitat associations indicated vulnerability following expected alterations from sea level rise. Black rails occupied 17 of 344 sites surveyed. Landscape factors had the strongest influence on black rail occupancy. Occupancy was significantly associated with impounded marshes, increasing distance to forest, and greater proportion of marsh landscape within a 200 m buffer. We mapped parameters from our top-ranked model to predict the amount of current and future suitable habitat under various sea level rise scenarios at Bear Island Wildlife Management Area, a black rail hotspot. Suitable habitat decreases in tidal marshes but increases in impounded areas. The current use of impoundments by black rails could represent a new management strategy for mitigating the loss of black rail habitat. However, assessing vulnerability is often difficult because predictions made in space or time may not always hold up. Therefore we evaluated how well species-habitat models derived in one locale would transfer to another in an effort to promote effective species-habitat conservation across a region (between states).

Species distribution models have been applied across a wide range of spatial scales to generate information for conservation planning. But the generality of these

models has rarely been tested. When transferability of models is evaluated it is typically done using occurrence data. However, we assess model transferability in coastal tidal marshes of the Southeastern United States using point counts of a widespread marsh bird: the clapper rail (*Rallus longirostris*). We first derived the top species-habitat models at a state-level in both South Carolina and Georgia, and then assessed how well top models from each state predicted abundances across the region (between states). Internally (locally) validated models exhibited reasonable fit and high significance; however, during the independent model validation process (between states) both models performed poorly. We discuss potential reasons model transferability was not successful and address the need for better regional datasets and further studies addressing issues associated with transferability.

Overall, coastal wetlands are some of the world's most productive and ecologically valuable habitats but they remain greatly disturbed. Understanding the influence potential disturbances, such as sea level rise and development, will have on wildlife species is critical toward helping to promote effective conservation of coastal ecosystems.

DEDICATION

I would like to dedicate this thesis to my family who has supported me continuously throughout the pursuit of my dreams and crazy adventures. I would also like to recognize all the conservationists across the world that work tirelessly to make a difference; I hope to join your ranks one day.

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CHAPTER ONE

MANAGED HABITATS INCREASE OCCUPANCY OF BLACK RAILS (*LATERALLUS JAMAICENSIS*) AND MAY BUFFER IMPACTS FROM SEA LEVEL RISE

INTRODUCTION

Global wetland degradation and loss is occurring at a rapid rate, and in the United States alone over 50% of wetlands in the lower 48 states have been lost since European settlement (Dahl 1990). Most of this loss is due to draining, ditching, and conversion to agricultural lands (Tiner 1984); however, additional stressors such as climate change and urbanization also greatly impact aquatic systems by fragmenting landscapes and reducing habitat quality (Meyer et al. 1999, Wang et al. 2001, Lee et al. 2006). Nevertheless, loss of wetlands is not always permanent. In some cases, wetlands that were historically altered for agriculture have been reclaimed and are managed as wetland habitat again. These managed habitats provide opportunities to create more complex landscapes than non-managed landscapes creating suitable habitat for various wetland-dependent species. For example, proper forest stand management has increased ephemeral wetland persistence, which resulted in regional increased diversity of amphibian species (Lehtinen et al. 1999, Russell et al. 2002). Managed habitats such as rice fields have been attributed to persistence of endemic and migratory avifauna in North America, Europe, and Japan (Maeda 2001, Elphick 2004, Sánchez-Guzmán et al. 2007, Fujioka et al. 2010). In Japan over 30% of native avian species use rice fields throughout their lifetime (Fujioka et al. 2010). Altered landscapes, in the form of managed wetlands, can allow for more complex landscape structure and can increase conservation efforts in an area by allowing managers

to incorporate learned strategies into effective management – a valuable tool as habitats become fragmented or lost.

Coastal wetlands are particularly vulnerable to anthropogenic disturbances such as increased development and rising seas. Furthermore, these wetland ecosystems are vulnerable to changes because they link marine, freshwater, and terrestrial habitats together, are highly productive, support high numbers of endemic species (Greenberg et al. 2006), and are highly disturbed. Because of the ecological value of coastal systems and the significant threats they face, conservation efforts are urgently needed that will highlight important current and future habitat for marsh specialists. The greatest concentration of tidal marsh in the world occurs in the Southeast and Gulf Atlantic coastal regions of the United States (Greenberg et al. 2006). In this region the coastal landscape is fairly complex containing a mix of habitats including tidal and managed marshes (impoundments), pine forests, and bottomland swamps (Wharton et al. 1982). In coastal South Carolina, managed impoundments occur frequently amongst unmanaged tidally-influenced marshes. Rapid tidal marsh loss is occurring in the Southeastern United States with predictions of 20-45% of coastal marsh being lost in South Carolina and Georgia by 2100 as a result of sea level rise (Craft et al. 2009).

Rising sea levels can increase the physiological stress of wetland plants and ultimately alter the community structure and biodiversity within a wetland (Baldwin et al. 1996, Baldwin and Mendelssohn 1998). Managed impoundments may buffer adverse effects from sea level rise by providing new and diverse landscapes that can be managed for species-specific conservation actions. Hydrological inputs within an impoundment are

controlled by structures called rice trunks, which allow designated amounts of water to flow in and out during tidal fluctuations. Since managers can alter the wetland hydroperiod and therein the succession of an impoundment, they can influence the plant, invertebrate, and vertebrate composition. Although historically managed impoundments have primarily provided habitat for waterfowl and shorebirds (Gordon et al. 1998, Colwell and Taft 2000, Taft et al. 2002) they can attract non-target species such as marsh birds (Brown and Dinsmore 1986, Koper and Schmiegelow 2006, Ma et al. 2010); a group especially sensitive to habitat changes because their life cycle is almost entirely dependent on wetlands.

Nine species of the marsh bird family *Rallidae* breed in North America, and all nine [(black rail (*Laterallus jamaicensis*) yellow rail (*Coturnicops noveboracensis*), clapper rail (*Rallus longirostris*), king rail (*Rallus elegans*), sora (*Porzana carolina*), virginia rail (*Rallus limicola*), purple gallinule (*Porphyrio martinicus*), common gallinule (*Gallinula galeata*), and american coot (*Fulica americana*)] can be found using South Carolina coastal wetlands during one or more parts of their life cycle. The *Rallidae* family is the second most diverse waterbird group (after *Anatidae*) with ~140 species (Eddleman et al. 1988, Reid 1993, Tori et al. 2002). Marsh birds are valuable indicators of marsh ecosystems because they occupy high trophic levels (Rush et al. 2009), and their life cycle is entirely dependent upon marsh ecosystems. These species require intact marshlands to persist, so loss of estuarine wetlands is the biggest threat to rail populations (Eddleman et al. 1988). Studies have reported up to 50% of global coastal wetland loss over the next fifty years (Nicholls et al. 1999, Zedler and Kercher 2005). An alarming

rate because over half of South Carolina's species of special concern inhabit within 3 m of mean sea level, including six species of federally threatened coastal birds (Daniels et al. 1993). Therefore understanding current habitat associations of marsh specialists, such as rails, allows us to evaluate their vulnerability to projected changes in currently occupied habitats.

We chose to study the black rail because they are habitat specialists, a species of special concern in South Carolina, and their populations along the Atlantic coast have been anecdotally declining (pers. comm Michael Wilson). Lack of knowledge about their life history and their secretive behavior makes them difficult to study, and what scientists do know is mostly limited to vocal records (Eddleman and Legare 1995, Evens and Nur 2002, Conway et al. 2004, Spautz et al. 2005, Conway and Gibbs 2011). Such secretive behavior has resulted in this species remaining one of the most understudied marsh birds in North America and their seemingly stringent habitat requirements make it a good candidate for understanding the role of heterogeneous habitats in long-term conservation planning for coastal marshes. Thus, there remains an urgent need to catalog black rail habitat associations in the southeast in order to enact effective management and conservation strategies.

Our primary objective was to assess the habitat associations and subsequent vulnerability to sea level rise for black rails. Because of the prevalence of managed impoundments within our study area, we were also able to evaluate the value of these habitats for black rails, and therein assess appropriate management strategies for non-target species. We assessed landscape and local environmental factors that might predict

black rail occupancy in South Carolina. Understanding habitat associations can provide insight into the benefits of various habitat types for species-specific conservation. Furthermore, habitat associations coupled with existing sea level rise models offer a starting point for assessing long-term species and habitat resilience.

METHODS

Study area

We conducted occupancy surveys for black rails at 344 survey sites, in 250 km² of South Carolina coastline, in five counties (Georgetown, Charleston, Colleton, Beaufort, and Jasper) (Fig. 1.1). The majority of survey sites were located in the Ashepoo-Combahee-Edisto (ACE) Basin region (1416.4 km²) one of the largest undeveloped estuaries along the Atlantic coast. The ACE Basin is composed of unmanaged tidal marsh, managed impoundments, and coastal plain forests. We conducted surveys during the 2014 breeding season (April-July) of marshlands on federal, state, and privately owned property. Survey points were selected based on *a priori* hypotheses for areas deemed appropriate black rail habitat (Flores and Eddleman 1995, Legare and Eddleman 2001, Tsao et al. 2009, Richmond et al. 2010), historical occurrences (Cely et al. 1993) or survey sites, and previous black rail accounts (ebird.org). We targeted high marsh, fresh and brackish emergent wetlands with low flooding impact (< 1 m). Habitats consisted of marsh grass (*Spartina bakeri/patens*, *Schoneoplectus americanus/robustus*, *Juncus roemerianus*) and shrubby bushes *Baccharis hamifolia* at elevations mostly > 0.5 m (Table 1.1) with water levels < 5 cm. We also noted the presence of other marsh bird species of concern including seaside

sparrow (*Ammodramus maritimus*), least bittern (*Ixobrychus exilis*), king and clapper rail, and marsh wren (*Cistothorus palustris*).

Study design

All surveys were conducted in the evening, three hours prior to sunset to a half hour post sunset (Spear et al. 1999, Legare et al. 1999, Conway et al. 2004). Each site was located at least 150 m apart because it can be difficult to hear black rail calls past 100 m (Conway et al. 2004). We conducted three repeated occupancy surveys at all sites, with a minimum of 10 days between consecutive surveys. We broadcasted black rail vocalizations in to the marsh (Legare and Eddleman 2001, Conway and Gibbs 2005) using MP3 players and Radio Shack Mini Audio Amplifier 90db. We used an eight minute playback sequence consisting of a two minute passive period, followed by two minutes of vocalizations (*kik-kee-doo* and *churt* calls for 30 seconds followed by 30 seconds of silence, played in a repeated sequence), followed by four more passive minutes (Legare and Eddleman 2001). Twenty-five observers conducted surveys, with one or two observers present during each survey. Each observer attended a black rail survey workshop prior to conducting surveys. When possible, surveyors alternated routes during each survey so points were not surveyed at the same time during each of the three visits. We did not conduct surveys during periods of sustained rain or when wind speed was greater than 25km/h.

In addition to data on black rail presence, we also recorded habitat variables at landscape and local scales. We obtained landscape variables using ArcGIS 10.2 (ESRI; Redwoods, CA). We used land cover data from Sea Levels Affecting Marshes Model

(SLAMM 5; <http://warrenpinnacle.com/prof/SLAMM>), which incorporate data from the National Wetlands Inventory, digital elevation models, sedimentation and accretion rates, and various other wetland scenarios. At the landscape scale, nine variables were recorded for all sites including patch size [total area (m^2) of the marsh which contained the sample point], edge density or the amount of marsh-water interspersions, proportion of marsh landscape within a 200 m buffer for each of three marsh categories (fresh + brackish + salt), proportion of brackish marsh within 200 m buffer, proportion of fresh marsh within 200 m, distance to development (m) and forest (m), average elevation (m) within a 200 m radius, and management activity (tidal vs. impounded). To obtain the patch area (m^2) for the marsh we examined the combined area of fresh, brackish, and salt marsh as defined in the SLAMM 5 dataset. We calculated edge density or marsh/water interface using FRAGSTATS. To calculate proportion of brackish, fresh, and total marsh (fresh + brackish + salt) marsh we used neighborhood and focal statistics tools in ArcGIS 10.2 to sum the raster cells of brackish/fresh marsh within 1 x 1 m window within a 200 m radius. We used the Euclidean distance tool to obtain the closest distance (m) from our survey point within a 200 m buffer to developed or forested areas. Elevation data were downloaded from the National Elevation Dataset (NED; <http://ned.usgs.gov>) with a 1/3 arcgrid 10 m resolution. To obtain elevation we used the resample tool to get a mean elevation within a 200 m buffer of our survey point. Classification of management activity at sites (managed impoundments vs. tidally influenced areas that are not managed) was done during site visits and further verified using Google Earth (<https://www.google.com/earth/>). All raster files were set to the same spatial extent and

were analyzed within a 30 x 30 m grid size. Additionally we standardized all covariates by mean and removed highly correlated variables.

Because of the effort and expertise required to collect data at local scales, we only obtained these data at 147 of 344 sites, including all occupied sites and sites with high accessibility. Local data included plant species composition, average height of vegetation (m), percent cover of four common taxa (*Spartina alterniflora*, *J. roemarianus*, *S. patens*, and *Schoneoplectus spp*), and average water level (cm) within a 50m radius of the sample point. Our vegetation height covariate was an index of all vegetation cover at the survey site. We classified height of vegetation as follows 1 = <0.5 m, 2 = 0.5-1.5 m, 3 = > 1.5 m. We then multiplied the percent cover of each species by their vegetation height category and added them all together to obtain a weighted measurement of total vegetation height at a site.

Data analysis

We conducted single-season occupancy models using Program PRESENCE 6.9 (U.S. Geological Survey) to estimate detection and occupancy probability of black rails as a function of recorded covariates during the 2014 breeding season. We selected a single-season approach because detection probabilities for black rails are likely to be low and variable across samples (Legare et al. 1999); ignoring this fact could lead to severely biased estimates of occupancy (MacKenzie et al. 2002). We ranked models using corrected Akaike's Information Criterion values (AIC_c). Models with a delta AIC_c of less than two were deemed competitive (Burnham and Anderson 2002).

We conducted analyses in a step-wise fashion (Meents et al. 1983, Conway and Sulzman 2007) first independently assessing detection probability (344 sites), then the influence of landscape habitat variables (344 sites), the influence of local habitat variables (147 sites), and lastly the combined local and landscape variables (147 sites). We began by assessing the role of six different covariates we identified as potentially influencing detection probability. Detection covariates were collected during each survey and included: sky (clear or variable sky), background noise (none/minimal noise vs. moderate/high noise), wind (none to minimal wind vs. moderate/high winds), Julian date, and observer (expert vs. novice). An observer was deemed “expert” if he or she had previous experience surveying black rails. To identify the most important detection covariates, we constructed models that allowed detection to vary as a function of one or more of the above variables. The detection covariate(s) included in models with a $\Delta AIC_c < 2$ were included in subsequent models that focused on habitat factors influencing site occupancy. We then constructed candidate models using landscape-only and local-only habitat covariates for occupancy. Again, those variables appearing in models with a $\Delta AIC_c < 2$ were retained for a final candidate model set that included both local and landscape factors. We calculated a receiver operating characteristic area under the curve (AUC) statistic plot to assess the goodness of fit for our top landscape and combined models (Fielding and Bell 1997, Syphard and Franklin 2009).

Finally, we used the mappable parameters from the combined analysis dataset to identify the amount of current and future habitat (2050 SLAMM data) in order to prioritize current critical black rail habitat throughout the state and predict future

vulnerability. Using ArcGIS 10.2, we evaluated the changes in these top parameters under varying sea level rise scenarios and therefore the potential vulnerability of black rails to sea level rise impacts. Sea level rise scenarios were derived from the Intergovernmental Panel on Climate Change (IPCC) emissions scenarios. For our combined model the only mappable parameter in South Carolina is the proportion of marsh habitat within 200 m radius. The mean value for this parameter at occupied sites was 69.65 ± 10.07 . We deemed habitat suitable if the proportion of marsh landscape was greater than 60% within a 200 m radius of a given 30 x 30 m mapped cell. We used a conservative estimate because occupancy probabilities increase slightly from 10-20% at greater than 60% proportion of marsh (Fig. 1.3). Anything less than 60% had less than 10% occupancy probability. Thus black rails may not necessarily require vast contiguous habitat but rather the appropriate type of habitat.

We selected a fossil fuel intensive A1FI and moderate A2 emissions scenario (IPCC 2007), to provide estimates for habitat loss under varying model emissions. While there are no state-wide maps of managed impoundments in South Carolina we obtained maps of managed impoundments from Bear Island WMA (Fig. 4). Bear Island WMA is located in the ACE Basin, which is comprised of managed impoundments and large swaths of undeveloped tidal marsh. We mapped current and future marsh habitat in locales where the proportion of marsh habitat within 200 m of a survey site was $> 60\%$. Additionally, over half of our occupied sites were located on Bear Island WMA, a historic known location of black rail occupancy.

RESULTS

Distribution

We detected black rails at 17 of 344 sites throughout South Carolina (Fig. 1.1). Five sites were recorded on the Tom Yawkey Wildlife Center, one on Santee Coastal Reserve, one at ACE Basin National Wildlife Refuge, one on Hutchinson Island, eight on Bear Island Wildlife Management Area (WMA), and one on the upper Ashepoo River. Eleven of the 17 occupied sites occurred in the southern portion of the state, primarily in the ACE Basin. We surveyed 176 unmanaged tidal marsh and 168 non-tidal impounded marshes. Fourteen of the occupied locations occurred in non-tidal impounded marshes.

Detection and Habitat Variables Influencing Black Rail Occupancy

We evaluated six potential covariates for detection probability, including the null and global model. The only competitive model was the effect of observer (expert vs. novice). Detection probabilities were twice as high for expert observers versus those who were considered novice in the landscape analysis (0.20 vs. 0.04). All models of occupancy were examined using observer (expert/novice) as a detection probability covariate.

From our initial landscape analysis, at 344 sites, we selected competitive models ($\Delta AIC_c < 2$; Table 1.2) influencing black rails habitat selection. These top models included five parameters: management activity (tidal vs. impoundment), the proportion of marsh habitat within a 200 m radius, distance to forest (m), elevation (m), and the patch size of marsh habitat (m²; patch area) of the entire patch of marsh where the survey point was located (Table 1.2). However, the only significant relationship (95% confidence

intervals did not include zero) was with management activity. All top models included the parameter management activity in them (Table 1.2). Unmanaged tidal marshes were negatively associated with black rail occupancy; 14/17 occupied sites were located in managed impoundments and the odds of occupancy at impoundments were estimated to be four times that of tidal marshes. Black rail occupancy decreased as distance to forest (m) and elevation (m) increased. Additionally, black rail occupancy increased as the proportion of marsh habitat within a 200 m radius increased and as patch size of marsh habitat increased. Our top model for the landscape candidate model dataset included management activity and distance to forest (Fig. 1.2). Proximity to forest may also represent a preference for higher or sloping elevations, although no habitat covariates were correlated. The AUC value for the top landscape model was 0.70.

The analysis of local habitat variables was conducted on candidate model dataset of 147 sites, including all occupied locations (Table 1.3). Covariates from top models were vegetation height (m) and percent cover of *S. bakeri/patens*. Black rails had a weak positive association with tall vegetation of half a meter or greater and high percent cover of *S. bakeri/patens*. Covariates from top models ($\Delta AIC_c < 2$) in the landscape and local analysis were then combined to assess multi-scale factors influencing black rail occupancy. Top models from our combined analysis included four parameters: management activity, proportion of marsh habitat within a 200m radius, distance to forest (m), and average vegetation height (Table 1.4). The only significant effect was the influence of management activity, such that black rails were positively associated with managed impoundments. This variable was again included in all top models. Rails were

positively associated with taller vegetation heights, higher proportion of marsh habitat within 200 m, and proximity to forest. Models with only landscape variables were the most competitive; however, local variables appear to have some influence during black rail site selection. The percent cover of *S. bakeri/patens* and vegetation height was weakly but positively associated with occupancy of black rails (0.06 ± 0.32 and 0.24 ± 0.44 respectively). The top combined model, which includes tidal and proportion of marsh landscape (Fig. 1.3), highlights black rails use of primarily managed impoundments and higher proportion of marsh habitat ($> 69\%$) within a 200 m radius around a survey point. The AUC value for the top combined model was 0.71, suggesting that the landscape covariates explain the vast majority of variance.

Mapping conservation hotspots and future sea level rise vulnerability

In order to identify appropriate black rail habitat throughout the state we used the top model of combined local and landscape variables. Under a 2050 fossil fuel intensive-A1FI model there was a net gain of marsh habitat within Bear Island WMA (Fig. 1.4). Both A1FI and A2 2050 emissions scenarios for Bear Island WMA impoundments showed an approximately 5% increase in suitable black rail habitat. The majority of marsh gain was within managed impoundments where marsh vegetative coverage shifted or expanded. At a broader scale, we observed a net loss of total marsh habitat within the ACE basin boundary lines by 12% and in North Inlet-Winyah Bay National Estuarine Research Reserve (NERR), where marsh is primarily unmanaged and tidally influenced, there was a net loss of marsh by 32%. The losses in the ACE Basin and specifically at

Bear Island WMA occur primarily in tidal marsh (Fig. 1.4). Furthermore, in our entire study region there was a 5% net loss of marsh by 2050.

DISCUSSION

Detection

Currently, black rails along the Atlantic coast exist as small, patchily-distributed populations. Our results show that expert observers are twice as likely to detect a black rail than novice observers. Previous avian studies have demonstrated that detectability varied with observers (Farnsworth et al. 2002, Diefenbach et al. 2003, Thomson et al. 2009). Detection probability should be explicitly accounted for since it can be difficult to detect population trends and habitat associations when detectability is low. Accounting for observer experience, as we have done here, will likely enhance survey efforts associated with secretive marsh birds, potentially increasing the number of detections. It is worth noting that expert observers surveyed Bear Island WMA, an area of historic black rail frequency in South Carolina. Because only expert observers were associated with this hotspot our estimates of observer effect are potentially overestimated. However, 50% of the additional occupied black rail sites were detected by novice observers, therefore we believe this potential source of bias was minimized. Our low sample size of occupied sites could reflect low detectability of black rails, low population size, or poor site selection, although we do not believe it to be attributed to the latter as many regional experts were consulted during the site selection process.

Distribution and habitat use

Black rails were not distributed homogenously across the landscape but rather localized, primarily in the ACE Basin and in the northern region of the South Carolina coast on the Tom Yawkey Wildlife Center (Georgetown County). The majority of rails found in our study were located on state or federal lands (88%). Similarly, Cely and colleagues (1993), also found that black rails were localized along the coast of South Carolina, primarily at the Tom Yawkey Wildlife Center (Yawkey), Santee Coastal Reserve (SCR), and Bear Island WMA. The above properties maintain vast sections of managed impoundments. During these previous surveys black rails were associated with unmanaged marshes (46%) and managed marshes (54%). In our study black rails primarily used managed impoundments (82%), potentially representing a shift in habitat preference toward managed impoundments. Most impoundments are managed for waterfowl and shorebirds; however, the few that are not species-specific can develop dense vegetation growth that supports non-target species like black rails. Additionally, maintaining shallow water levels in impoundments that are not targeted for waterfowl may further enhance breeding habitat for dwindling black rail populations (Legare and Eddleman 2001, Richmond et al. 2010). The high frequency of impoundments in South Carolina represents a previously unreported opportunity to enhance black rail conservation in the southeast through appropriate management and continued regionally coordinated efforts. However, it will be important to expand upon knowledge of black rail distribution by evaluating demography within the state of South Carolina.

Black rail habitat use in South Carolina is similar to other locales in that birds selected areas with tall marsh grasses (*Spartina bakeri/patens*, *Baccharis hamifolia*,

Schoenoplectus robustus/americanus). The three unmanaged tidal habitats that had black rails occurred in high marsh areas with brackish type vegetation (*S. americanus* and *Typha spp*). Other studies have also highlighted the importance of vegetation density (Tsao et al. 2009) but we did not assess this variable at our sites. Shallow water level is generally a key determinant for appropriate habitat for black rails (Flores and Eddleman 1995b, Eddleman and Legare 1995, Richmond et al. 2010); however, because we targeted primarily shallow water habitat (< 5 cm) we excluded water levels from the analysis. Moreover, 88% of sites were located in habitats with an average water level of < 3 cm. Large patch sizes were positively associated with black rail occupancy indicating black rails may prefer larger habitats which supports findings in other states (California) (Spautz et al. 2005).

Since previous comprehensive studies of black rails in the southeastern United States are scarce, and most information has been anecdotal, information of rail life history and habitat use is usually restricted to more abundant and less secretive rail species such as virginia, yellow, and sora rails (Conway et al. 1994, Haramis and Kearns 2007, Martin et al. 2014). Knowledge of coastal habitat associations with rails is infrequent, but black rail populations in the Northeastern U.S. are presumed to use tidal marsh and inland moist fields (Kerlinger and Wiedner 1991). Unlike tidal marshes, managed impoundments provide some protection from climate impacts and can be managed for specific species. Our findings represent an important conservation management tool that could enhance black rail resilience to sea level rise and development. Additionally, the ACE Basin contains large tracts of undeveloped federal,

state, and privately owned land in conservation easements. These properties make the area less susceptible to developmental pressures. Existing impoundments in the ACE Basin coupled with lower developmental pressure may make this locale a premiere conservation hotspot in the future.

Black rails are a species of special concern in South Carolina, but we also documented a suite of species using the same impoundments as black rails including: seaside sparrow, least bittern, king and clapper rail, and marsh wren. These are primarily marsh-obligate species and represent the range of diversity these managed impoundments can support in addition to traditional game species that are the targets of habitat management. Many of these secretive birds use habitats with shallow water levels < 15 cm and dense vegetation, particularly for breeding, where nests are built above ground to withstand flooding events (Gaines et al. 2003). Impoundments could be used to help provide refuge throughout the year for resident and migratory rails. Actively managing impoundments that are not currently being managed for waterfowl or shorebirds will not conflict with landowner's goals to continue to manage for waterfowl. Sea level rise threatens a wide range of coastal species, and managing impoundments for black rails may enhance the overall diversity and resistance of coastal ecosystems.

Loss of tidal marsh

The losses of tidal marsh may have negative consequences for marsh birds including black rails. As tidal habitats disappear, competition for resources, particularly food and breeding site selection, may become heightened in impounded areas. We observed seaside sparrows nesting in the same habitats used by black rails on Bear Island

WMA. Depletions in tidal marsh habitat may have secondary negative consequences for black rails, including reduction in foraging or wintering habitats. Moderate losses or migration of tidal marsh inland is expected to occur in the Southeastern U.S. (Craft et al. 2009, Brittain and Craft 2012) . Additionally, many sea level rise projections demonstrate a shift in upland marsh vegetative regime where salt marsh replaces brackish and freshwater marshes (Olff et al. 1997), which seem to be preferred marsh habitat for black rails in South Carolina. Alterations in sediment loads, salinity, and vegetation can alter the community structure of these ecosystems. In the Northeastern U.S., studies have predicted high marsh will be converted to forbs and stunted salt marsh grass (*S. alterniflora*) (Warren and Niering 1993). If these marshes are converted to more saline environments, with concomitant structural changes in vegetation or water level, they may become unsuitable for black rails and lead to further reductions in site occupancy and consequently population size. Variability in marsh accretion and subsidence estimates from the Northeastern and Southeastern Atlantic coast make regional vulnerability assessments difficult (Morris et al. 2002). Nevertheless, the use of managed habitats in South Carolina suggests this area could become a critical refuge for black rail productivity along the Atlantic coast.

Summary

Previous studies coupled with this research suggest a strong role for managed habitats in the conservation of a wide range of taxa not intentionally targeted by the management efforts. As sea levels rise and losses of tidal habitat become pronounced the importance of protected areas and managed habitats increases. Having the ability to

manipulate habitat and target high priority conservation areas is extremely important for the conservation of threatened species and biodiversity. Previous studies have identified the importance of managed habitats for wildlife. For example, managed forests in the coastal plain of South Carolina provide freshwater wetland habitat for a diverse assemblage of herpetofauna including four species of special concern (Russell et al. 2002). Additionally, managed impoundments in coastal South Carolina have higher species richness of fishes than nearby tidal creeks (Robinson and Jennings 2014); while many ducks and shorebird species use managed impoundments at higher frequencies than tidal marshes (Rundle and Fredrickson 1981, Weber and Haig 1996, Gordon et al. 1998). Collectively, these studies emphasize the importance of managed habitats for various taxa.

Coastal landscapes will continue to change as development pressure increases and sea levels rise. It is important to better understand species–habitat associations in order to protect critical habitat that will help ensure effective conservation of a target species or community. Coastal ecosystems are dynamic and complex, and if impounded structures are not maintained they will be subject to flooding and saltwater intrusion. It will require active state and federal involvement from land managers to ensure the upkeep of these structures. Knowing which species inhabit impoundments during critical life cycles such as breeding and migration will allow managers to effectively plan and create appropriate habitats.

Knowledge of species distributions and habitat associations can permit researchers and managers to prioritize conservation areas, which will assist future

management decisions and acquisition of high quality habitat. The persistence of a species is related to its local abundance, population growth, and their geographic distributions (Zuckerberg et al. 2009, Fleishman et al. 2014) thus continued monitoring and more detailed data collection is likely necessary for black rails and other marsh birds in this dynamic ecosystem.

Table 1.1 Environmental variable type, mean or range, and standard error for variables used in models to determine their influence on black rail occupancy in South Carolina.

Variable	Type	Mean/Range	± SE
Patch Area (ha)	continuous	1.82	± 0.037
Proportion of Brackish Marsh	continuous	20.04	± 1.61
Distance to Development (m)	continuous	1628.66	± 94.60
Distance to Forest (m)	continuous	186.03	± 16.71
Elevation (m)	continuous	0.95	± 0.031
Proportion of Marsh Landscape (brackish + fresh + salt)	continuous	60.06	± 1.27
Edge Density (interspersions)	continuous	90.50	± 2.37
Vegetation Height (m)	categorical	100-600; 266.18	NA
Tidal	categorical	0 or 1	NA
Percent Coverage of <i>Spartina bakeri/patens</i>	continuous	11.03	± 1.77

Table 1.2 Top candidate models from the full dataset with landscape covariates only. The influence of management activity on black rail occupancy appears in all top models as a significant variable. Black rails were negatively associated with tidal habitat, and 14/17 occupied sites were located in impounded areas

Model Name	ΔAIC_c	w_i	K	-2*LogLikelihood	Relationship (+/-)
$\Psi(\text{management activity} + \text{distance to forest})$ $\rho(\text{observer})$	0.00	0.26	5	168.18	(-/-) BLRA occupancy decreases in non-managed tidal marshes, and as distance to forest increases
$\Psi(\text{management activity})$ $\rho(\text{observer})$	0.12	0.24	4	170.36	(-) BLRA occupancy decreases in non-managed tidal marshes
$\Psi(\text{management activity} + \text{proportion of marsh cover})$ $\rho(\text{observer})$	0.71	0.18	5	168.89	(-/+) BLRA occupancy decreases in non-managed tidal marshes and increases as the proportion of marsh within a 200m radius increases
$\Psi(\text{management activity} + \text{patch area})$ $\rho(\text{observer})$	0.90	0.13	5	169.08	(-/+) BLRA decreases in non-managed tidal marshes and increases as patch area increases
$\Psi(\text{management activity} + \text{elevation})$ $\rho(\text{observer})$	1.54	0.09	5	169.72	(-/-) BLRA occupancy decreases in non-managed tidal marshes and in higher elevations
$\Psi(\text{management activity} * \text{distance to forest})$ $\rho(\text{observer})$	1.81	0.08	6	167.92	(-/-) BLRA occupancy decreases interaction of non-managed tidal marshes and distance to forest

Table 1.3: Top candidate models from the reduced dataset with local covariates only. These top models were carried into our final combined analysis to deduce the effects local variables had on black rail occupancy.

Model Name	ΔAIC_c	w_i	K	-2LogLikelihood	Relationship(+/-)
$\Psi(Spartina\ bakeri/patens)$ p(observer)	0.00	0.23	4	141.24	(+) BLRA occupancy increases as the amount of percent cover <i>S. bakeri/patens</i> increases
$\Psi(\text{vegetation height})$ p(observer)	0.76	0.16	4	142.00	(+) BLRA occupancy increases as vegetation height increases
$\Psi(Spartina\ alterniflora)$ p(observer)	0.94	0.15	4	142.18	(-) BLRA occupancy decreases as the percent cover of <i>S. alterniflora</i> increases
$\Psi(Juncus\ roemerianus)$ p(observer)	1.22	0.13	4	142.46	(+) BLRA occupancy increases percent cover of <i>J. roemerianus</i> increases
$\Psi(Schoeneoplectus\ spp)$ p(observer)	1.24	0.13	4	142.48	(+) BLRA occupancy increases as the amount of percent cover <i>Sch. spp.</i> increases
$\Psi(Spartina\ bakeri/patens + \text{vegetation height})$ p(observer)	1.41	0.12	5	140.5	(+/+) BLRA occupancy increases as the amount of <i>Spartina bakeri/patens</i> and vegetation height increases
$\Psi(Spartina\ alterniflora + S. bakeri/patens)$ p(observer)	1.79	0.1	5	140.88	(-/+) BLRA occupancy decreases as the percent cover of <i>S. alterniflora</i> increases and increases as the percent cover of <i>S. bakeri/patens</i> increases.

Table 1.4: The top candidate models for the combined analysis with both local and landscape covariates. Landscape variables appear to be the most important in determining black rail occupancy. However, local variables have a weak but positive effect on black rail habitat selection.

Model Name	ΔAIC_c	w_i	K	-2*LogLikelihood	Relationship (+/-)
$\Psi(\text{management activity} + \text{proportion marsh cover}) \rho(\text{observer})$	0.00	0.28	5	135.74	(-/+) BLRA occupancy decreases in non-managed tidal marshes and increases in areas with larger proportion of marsh cover
$\Psi(\text{management activity}) \rho(\text{observer})$	1.03	0.17	4	138.92	(-) BLRA occupancy decreases in non-managed tidal marsh
$\Psi(\text{vegetation height} + \text{management activity} + \text{proportion marsh cover}) \rho(\text{observer})$	1.82	0.11	6	135.39	(+/-/+) BLRA occupancy increases with an vegetation height >0.5m and an increase in proportion marsh cover
$\Psi(\text{management activity} + \text{distance to forest}) \rho(\text{observer})$	2.09	0.10	5	137.83	(-/-) BLRA occupancy decreases in non-managed tidal areas, and as distance to forest increases
$\Psi(\text{percent cover of } \textit{Spartina bakeri/patens} + \text{management activity} + \text{proportion marsh cover}) \rho(\text{observer})$	2.13	0.10	6	135.70	(+/-/+) BLRA occupancy increases with high percent cover of <i>S. bakeri/patens</i> , decreases in non-managed tidal areas, and increases as proportion of marsh increases
$\Psi(\text{management activity} + \text{patch area}) \rho(\text{observer})$	3.06	0.060	5	138.80	(-/+) BLRA occupancy decreases in tidal areas, and increases as patch area increases

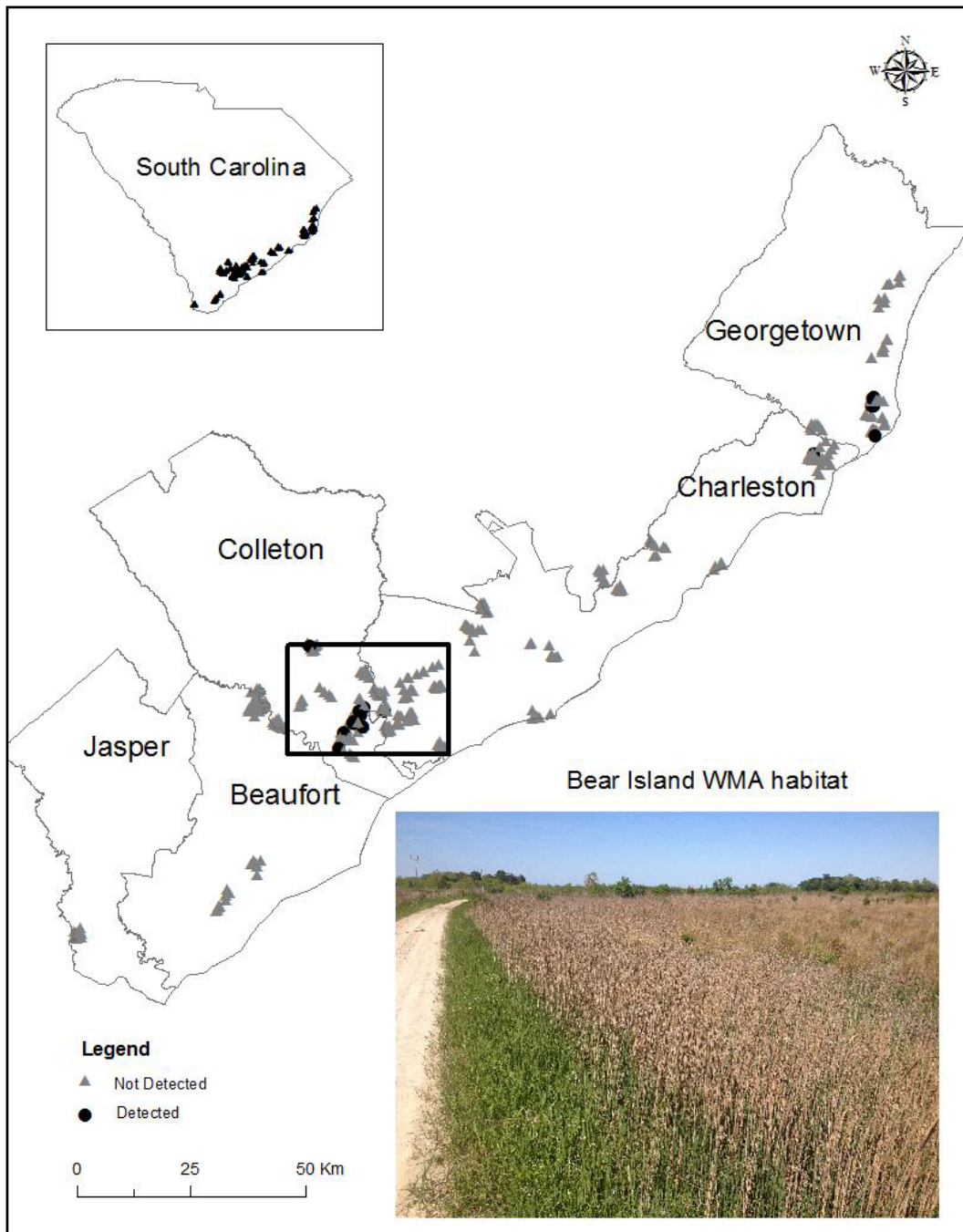


Figure 1.1 Black rail survey sites in South Carolina, United States. The majority of sites were located in the ACE Basin (denoted by the black box on the main map) and the majority of occupied sites were on Bear Island WMA. The photo in the bottom right exemplifies habitat of occupied locations.

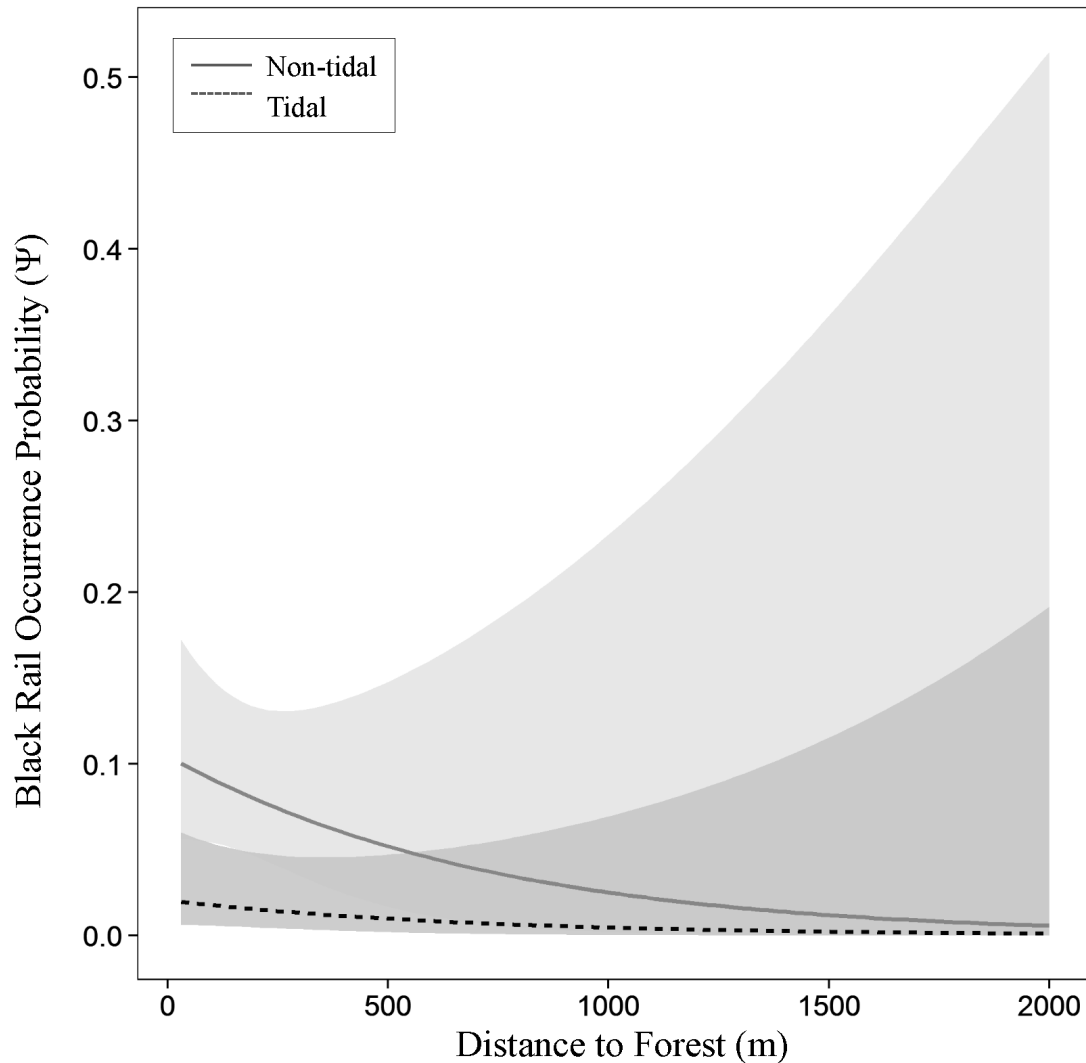


Figure 1.2 Black rail occupancy probability as a function of management activity and distance to forest (the top landscape model as estimated from 344 sites in South Carolina, USA). As distance to forest increased the probability a black rail occupancy at a site decreased. Black rail occupancy was higher in non-tidal areas across all values of distance to forest.

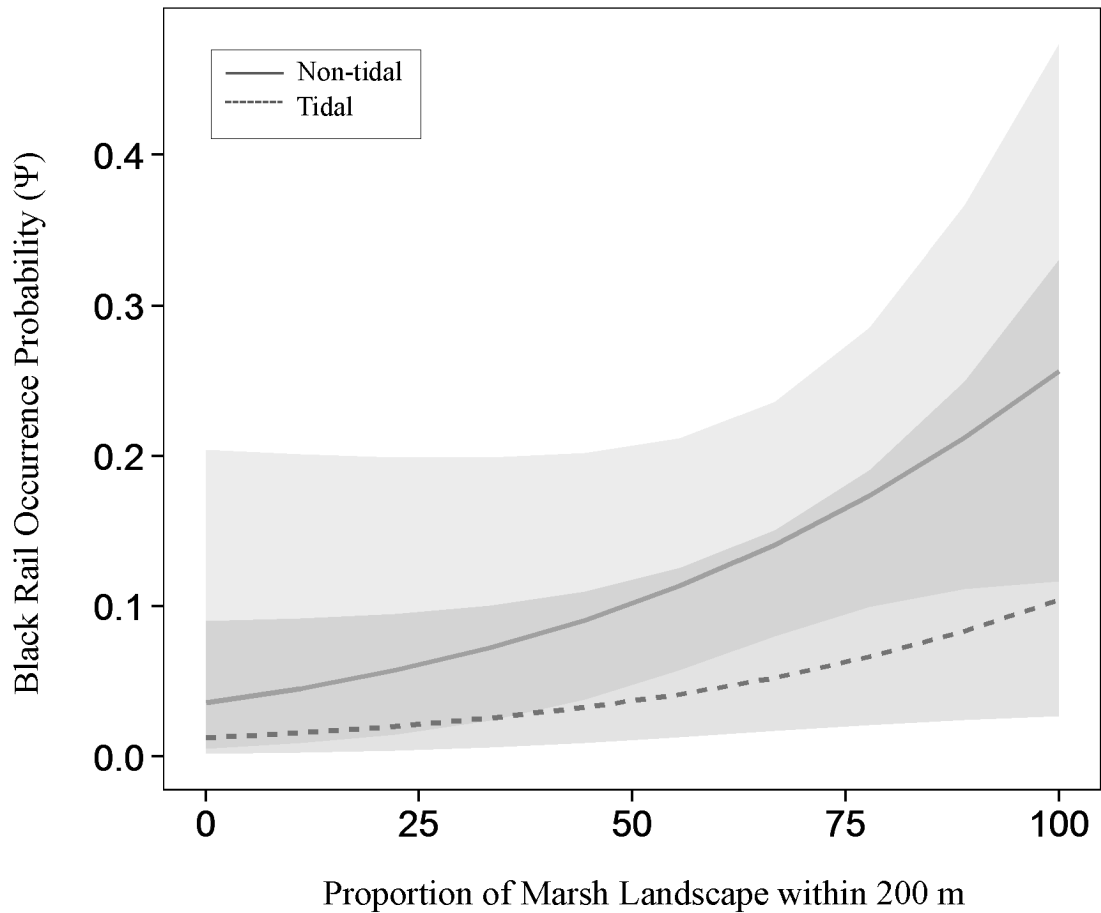


Figure 1.3 Black rail occupancy probability as a function of management activity and proportion of marsh landscape within 200 m (top model when local and landscape variables were combined across 147 sites in South Carolina, USA). Black rail occupancy increased as the proportion of marsh landscape within a 200 m radius increased and in non-tidal marshes. Black rail occupancy increases from 0.0 – 0.1 at ~ 60% marsh coverage within a 200 m survey point.

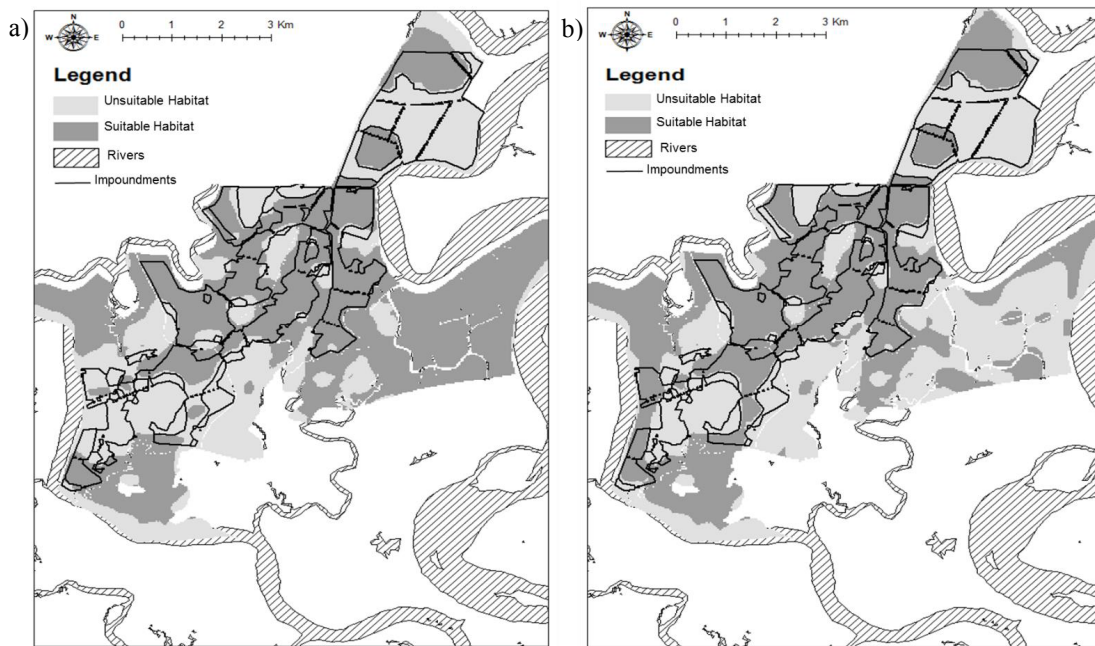


Figure 1.4 Current (a) and future (b) black rail habitat at Bear Island Wildlife Management Area in South Carolina, USA. Habitat was deemed suitable if proportion of marsh landscape was $> 60\%$, and unsuitable at lower values. Future habitat represents a projected scenario under a 2050 fossil fuel intensive A1FI scenario. Note that loss of suitable habitat outside of impoundments (e.g., far eastern portion of figure) are extensive, whereas very little suitable habitat is lost within the managed impoundments.

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CHAPTER TWO

ASSESSING TRANSFERABILITY OF HABITAT MODELS FOR A WIDESPREAD MARSH BIRD IN THE SOUTHEASTERN UNITED STATES: IMPLICATIONS FOR CONSERVATION PLANNING

INTRODUCTION

Knowledge of species-habitat relationships can shape management decisions (Pearce and Lindenmayer 1998; Raxworthy et al 2003; Engler et al 2004; Guisan and Thuiller 2005) and support conservation planning (Ferrier 2002; Araújo et al 2004). As landscapes become increasingly altered due to land-use and climate change, there is a growing need to understand species-habitat relationships across spatial scales. Insight into how well species-habitat models derived in one region will transfer to an independent region is preferable to the assumption that models will perform well with a new dataset or spatial scale. Thus it is important to measure the effectiveness of current habitat models and their ability to transfer in space and time. For example, studies of plants demonstrated that non-endemic species with higher dispersal activity had higher temporal transferability than endemic species with limited dispersal traits (Dobrowski et al. 2011). This information was then applied to future habitat models within the region. Additionally difficulties in transferability arise when there are differences in species demographics and productivity between regions (Gray et al. 2009); or when there are various levels of spatial heterogeneity amongst ecological relationships. Lastly, adjacent geo-political lines, such as countries and states, may not be ecologically similar and therefore it is important to consider the potential for localized adaptations that yield

unique species-habitat associations at the local scale. Such refined data may be necessary to enact effective conservation measures.

In general, projecting species distributions through space and time is challenging due to limitations with modeling approaches and understanding of how species may respond to environmental changes (Guisan and Zimmermann 2000; Dormann 2007; Vallecillo et al. 2009). There are a number of explanations for why models of species-habitat associations may fail to transfer well across space or time. Such models assume species are at equilibrium with their environments and that relevant environmental gradients have been adequately sampled (Fielding and Haworth 1995; Guisan and Zimmermann 2000; Whittingham et al. 2003; Norgues-Bravo 2009); however, many issues such as species invasions, climate change, and disturbances represent cases where species records are unrepresentative of equilibrium conditions (Elith and Leathwick 2009). Building predictive models that transfer to new geographic regions or times is difficult because areas targeted for model transfer may have unique combinations of environmental variables not represented in the model training region (Elith and Leathwick 2009). In order to achieve greater transferability, predictor variables should be ecologically relevant to the target species (Mac Nally 2000; Peterson and Nakazawa 2008; Rödder and Lötters 2010). Many current environmental datasets suffer problems from spatial and temporal autocorrelation, which can generate problems in the calibration and validation of species-habitat models (Araújo et al. 2005). Moreover, models assume immediate species response to climate change (Araújo et al. 2005) when in reality

dispersal limitations and alterations to networks of biotic interactions may prevent rapid evolutionary adaptations (Loehle and LeBlanc 1996; Pearson and Dawson 2003).

Species distribution models that transfer well across space and time would be particularly valuable in coastal marsh ecosystems. Many parts of these systems are relatively homogenous with respect to vegetation structure; however, a diverse suite of threats face coastal systems (i.e., sea level rise, coastal development, salt water intrusion, etc.). Furthermore, in the United States these systems are distributed across a wide latitudinal gradient, so it remains unevaluated how well models constructed in one place will predict species habitat use in other regions. Some of the most intact tidal marsh habitat in the world is found in the Southeastern United States (Greenberg et al. 2006), so this area represents a unique opportunity to evaluate model transferability across regions. Additionally, the impending threat of sea level rise would suggest a further need to critically evaluate transferability in coastal systems.

Marsh bird populations in North America have declined from habitat loss, and as a result of sea level rise these species are of special concern in many coastal states (Eddleman et al. 1988; Conway and Sulzman 2007). Given these threats, we selected the clapper rail (*Rallus longirostris*) as a representative species for evaluating model transferability in coastal systems. Clapper rails are relatively abundant along the Atlantic coast, where they spend their entire life cycle in salt marshes (Rush et al. 2010). Their life history and high trophic level make them an indicator of marsh ecosystem function (Rush et al. 2009). Clapper rails are a good candidate species for model transferability studies because they occupy tidal marshes throughout the Southeastern United States. We

assumed clapper rail populations were at equilibrium because patches of surveyed habitat included established breeding territories, with little to no prolonged disturbances. Moreover there have been no recent extreme climatic events that we believe would disrupt the equilibrium of this species in the southeast.

Our main objective was to assess what environmental variables influenced clapper rail abundance in the Southeastern United States (South Carolina and Georgia), and determine how well models would transfer across a region (within these two states). By collecting data from both South Carolina and Georgia we aimed to garner information about what predictor variables influenced within state abundance and assess if models could transfer through space (between states). This information could reduce uncertainties associated with conservation planning risks, as well as help determine suitable habitat for clapper rails in the southeast.

METHODS

Study area and site selection

We measured abundance of clapper rails across 250 km² of coastal tidal marsh in South Carolina and Georgia. Sites were selected based on representation of predominant environmental gradients and accessibility. Environmental variables such as patch size (m²), distance to forest and development (m), elevation (m), proportion of brackish marsh, proportion of marsh landscape (brackish + salt marsh), and edge density determined site selection. We surveyed 72 points in South Carolina and 214 points in Georgia. Survey points were located along marsh edge, separated by 400 m and accessed by boat. All surveys were conducted as close to the GPS location as possible but always

within 30 m from GPS locale. In South Carolina research sites were located within a 10-km² region on the North Santee River and Winyah Bay and within 12 km² of tidal marsh in the Ashepoo-Combahee-Edisto (ACE) Basin, one of the largest intact estuaries on the Atlantic coast. Sites in Georgia spanned 150 km² of salt marsh ranging from Savannah to St. Mary's rivers.

Study design

We used call-playback surveys to collect abundance data. Count surveys were conducted during the 2013 clapper rail breeding season, from sunrise to three hours afterward, during three survey periods: March 15 - April 15, April 15 - May 15, May 15 - June 15. We left at minimum of 10 days between consecutive surveys. We broadcasted marsh bird vocalizations using MP3 players and a Radio Shack Mini Audio Amplifier 90db. We derived our broadcast vocalization sequence from the 2009 Conway Marsh Bird Protocol (Conway 2009). Our playback sequence consisted of five passive minutes followed by three minutes of alternating vocalizations (30 seconds) and silence (30 seconds). We broadcasted vocalizations from three species throughout the three minute call sequence including: *kik-kee-doo* and *growl* for black rail (*Laterallus jamaicensis*), *tut-tut* and *gack-gack* for least bittern (*Ixobrychus exilis*), and *clapper*, *kek* and *kek-burr* for clapper rail. We included other marsh bird vocalizations in our playback because clapper rails are known to vocalize in response to heterospecific calls (Johnson and Dinsmore 1986; Allen et al. 2004; Conway and Nadeau 2010). We used a double observer method when conducting surveys (Bart et al. 2002). During each survey two observers independently recorded calls and abundances of clapper rails. We recorded

vocalization type, and clapper rail abundance at varying distances within a 200 m buffer from each site. By separating survey points by 400 m but only recording birds within a 200 m radius, we minimized detection of the same bird at adjacent survey points. We trained surveyors to estimate distances by playing calls throughout the marsh at various distances and having each observer estimate the distance to the playback prior to conducting surveys. We did not conduct surveys during periods of sustained rain or when wind speed was greater than 25 km/h.

Environmental variables

In addition to data on clapper rail abundance, we recorded data on landscape environmental variables. We gathered our landscape data from Sea Levels Affecting Marshes Model (SLAMM; www.warrenpinnacle.com/prof/SLAMM), which incorporates data from the National Wetlands Inventory, digital elevation models, and various wetland scenarios such as accretion, sedimentation, and inundation. SLAMM then generates models that evaluate sea level under varying climatic scenarios (including the current time). At the landscape scale, seven variables were recorded at each site. These variables included patch size [total area (m^2) of the marsh which contained the sample point], edge density (amount of marsh-water interspersions), proportion of marsh habitat within a 200 m buffer for two marsh categories (brackish + salt), proportion of brackish marsh within a 200 m buffer, distance to development (m) and forest (m), and average elevation (m) within a 200 m radius. To calculate edge density and proportion of marsh landscape we applied a FRAGSTATS analysis with a 200 m moving window. We used the euclidean distance tool (m) to obtain the closest distance from our survey point within a 200 m

buffer to developed or forested areas. We downloaded elevation datasets for South Carolina from the National Elevation Dataset (NED; <http://ned.usgs.gov>) with a 1/3 arcgrid 10 m resolution and for Georgia from the Georgia Department of Natural Resources lidar elevation at a 4-ft cell size that was aggregated to a 29-m cell size. To obtain elevation we used the resample tool to get a mean elevation within a 200 m buffer of our survey point. All raster files were set to the same spatial extent and were analyzed within a 30 x 30 m framework. We extracted values from the raster's to our survey points to get individual survey site landscape information. We standardized all covariates and tested for correlative variables.

Data analysis

We used R 3.1.0 statistical software, unmarked package, to analyze abundance data (Fiske and Chandler 2011). We selected maximum abundance as a metric because it is a better representation of species response to a predictor variable (Huston 2002) than data on presence-absence. We used the function “p-count” to fit N-mixture models to spatially and temporally replicated count data, while accounting for imperfect detection (Royle 2004). First we evaluated detection covariates in each state, next we evaluated the landscape variables influence on clapper rail abundance in each state independently and internally validated state models, and lastly we assessed how well models transferred between states through an external cross validation process. We began by assessing the role of six different covariates we identified as potentially influencing detection probability: sky (clear or variable sky), background noise (none/minimal noise vs. moderate/high noise), wind (none to minimal wind vs. moderate/high winds), Julian date,

observer, and tide type (rising/high vs. falling/low). To identify the most important detection covariates, we constructed models that allowed detection to vary as a function of one or more of the above variables. The detection covariate(s) present in models with a $\Delta AIC_c < 2$ were included in subsequent models that focused on habitat factors influencing site abundance. We used generalized linear models to assess the influence of detection and landscape covariates on abundance. We ranked models using corrected Akaike's Information Criterion values (AIC_c); models with a $\Delta AIC_c < 2$ were deemed competitive (Burnham and Anderson 2002).

To evaluate internal model performance we applied our top ranked model parameter estimates from each state to obtain predicted abundance estimates at each site within the same state from which the model was derived. To evaluate model transferability, we used the parameter estimates from the top model in one state to predict abundances at each site in another state. This created a total of four categories of model evaluation (two internal evaluations and two interstate evaluations). We used linear regression to compare the model-estimated (predicted) abundances to observed abundance data from the same locations for all four model evaluation scenarios. We accounted for detection probabilities at each site and used observed maximum abundances to evaluate model fit.

Using our parameter estimates from our top models we were able to predict specific areas deemed suitable habitat for clapper rails in South Carolina. Even if model transfer across regions poorly predicts absolute abundance, it is possible that transferred models still have utility to identify relative habitat suitability. To address this possibility,

we applied the South Carolina- and Georgia-derived parameters to habitat features in South Carolina and then identified the top 25% of tidal marsh habitat each model predicted within the state. Using ArcGIS 10.2, we applied the analysis only to the salt and brackish marsh designated by the initial SLAMM land cover in our study region. We then measured the overlap of habitat predicted between the models and considered that as an additional measure of model fit.

RESULTS

Detection probability and habitat variables influencing clapper rail abundance

Clapper rails occupied the majority of sites in both South Carolina (96%) and Georgia (88%). Our top model of detection covariates ($\Delta AIC_c = 0$) only included the presence or absence of wind during a survey. Detection probabilities varied among sampling occasions and were 0.32 and 0.23 in South Carolina and 0.30 and 0.22 in Georgia with no wind and wind respectively. After assessing all landscape variables in each state, with wind as our detection covariate, we evaluated models including landscape-level covariates of abundance for both states. In South Carolina the only competitive model ($\Delta AIC_c < 2$) was the interaction between distance to forest (m) and elevation (m) (Table 2.1). South Carolina clapper rail abundance was positively associated with distance to forest and negatively associated with elevation (Table 2.1). In Georgia the only competitive model was the interaction between distance to forest (m) and proportion of brackish marsh (Table 2.1). Georgia clapper rail abundance was negatively associated with distance to forest and proportion of brackish marsh, demonstrating a preference for less brackish marshes that were closer to forested areas.

We then internally-validated model performance by predicting abundances for each state using their top model parameter estimates and comparing them to the inflated observed abundances in their respective state. Each internal evaluation was significant ($p < .0005$), although total variance explained by predicted values was low ($R^2 = 0.36$ and 0.14 in SC and GA, respectively; Fig. 2a and 2d).

Model transferability

Models did not transfer well from state to state (Fig. 2b and Fig. 2c), as predictions using data from one state had poor fit and low R^2 values. Variability in the mean values of two of our top environmental predictors from each state, distance to forest and proportion of brackish marsh, may have explained why model transfer was so poor (Table 2.2). In order to further assess model fit we evaluated the suitable habitat each model predicted in South Carolina and examined the overlap between those two habitats. The South Carolina model was a more conservative estimate of habitat and identified 67% of the habitat as suitable in South Carolina whereas the Georgia model predicted 88% of the focal region as suitable in South Carolina. The overlap between the two suitable areas was 67%. Models from Georgia over-predicted potential high quality habitat in South Carolina.

DISCUSSION

This study demonstrates that model transferability should be assessed in areas where extrapolation to another region is a goal. This study also contributes to the literature on model transferability by assessing counts rather than presence/absence data. Our results indicate that even in a region where the landscape is fairly homogenous, local

(state) models are not necessarily transferable. One of the reasons for the poor transferability of models could be that our site selection for some variables did not reflect a gradient range that was similar in both states (Table 2.2). The average distance to forest and proportion of brackish marsh was markedly different in South Carolina and Georgia and our results may have been confounded by the dissimilarities between our distance to forest and proportion of brackish marsh sampling mean. Our results highlight the need to consider the local-scale (in this case at a state level) environmental variables from which a model is being applied, when predicting abundance for species in areas with regional differences or varying environmental conditions. Varying management strategies and historical uses in each state may have created local-scale landscape differences. For instance, South Carolina was heavily harvested for rice up until the early 20th century and remnant rice fields occur frequently throughout the coastline, breaking up the vast expanses of intact tidal marsh. Georgia on the other hand does not maintain impoundments at such a high frequency. Previous studies have shown that habitat relationships may exhibit regional variation for similar species in fairly homogenous-seeming landscapes (Whittingham et al. 2007). Additionally, when important ecological predictors are not included (or the value range of a predictor is not fully represented) in the modeling process, transferability may be compromised (Fielding and Haworth 1995; Graf et al. 2006; Randin et al. 2006; Varela et al. 2009). Other studies have documented the difficulties of including all environmental variability in models between regions. It will likely be more difficult to assess transferability if the data are not collected at the same scale, or if they are applied at varying spatial scales. All of the above issues

reiterate the importance of understanding and adequately sampling environmental variation across a region of interest.

Model transferability can also be impaired for a large number of logistical reasons in addition to the concerns of adequate sampling profiled above. In the southeast there are few congruent regional datasets, making it difficult to assess models across large regions. Large regional datasets that do exist can be mismatched with data collected on the ground. For instance some landscape data, such as SLAMM, poorly characterized sites we visited as part of this study. For example sites deemed salt marsh in our model were considered brackish marsh while collecting on the ground vegetative data. When such data are then used to construct regional models, the resulting product may not accurately reflect land cover values, which complicates conservation planning efforts at the local level.

While our models did not transfer well across space, the information we gathered at a state level can still be useful to conservation planners and help reduce uncertainties of species response to habitat loss associated with current and future anthropogenic disturbances. In the Southeastern U.S., many federal and regional wildlife agencies and land managers are interested in understanding the potential impacts sea level rise has on wildlife populations. Sea level rise is expected to alter habitats significantly in South Carolina and Georgia with rapid tidal marsh loss of 20 - 45 % projected for 2100 (Craft et al. 2009). Evaluating environmental variables that influence abundance of clapper rails in South Carolina and Georgia provides conservation planners information on key habitats for monitoring and protection. Species distribution models are often used in large-scale

conservation planning, but they may not be as effective if the habitat relationships or predictor variables are not appropriately understood. Transferability will likely be most effective when the training area is most similar to the test area; however, such conveniences may not be realistic in the context of real world conservation efforts spanning large regions or long time periods. This study demonstrates that there is a need to continue monitoring populations at a local scale because both local state abundances as well as habitat-abundance relationships differed in South Carolina and Georgia. Ecological systems are complex, so in addition to data collected across broad spatial scales we will also likely need long-term datasets to untangle some of those complexities.

Summary

Previous studies of model transferability have had mixed results. Accuracy of model predictions has varied across taxa (McPherson and Jetz 2007; Pöyry et al. 2008; Dobrowski et al. 2011) and modeling frameworks (Wenger and Olden 2012; Rapacciuolo et al. 2012). Studies using resource-based models, models incorporating phenological metrics, and models containing multi-year data have demonstrated high transferability (Vanreusel et al. 2007; Tuanmu et al. 2011). However most studies have observed only moderate ($AUC = 0.60-0.70$) transferability (Guay et al. 2003; Sundblad et al. 2009; Dobrowski et al. 2011; Tuanmu et al. 2011; Rapacciuolo et al. 2012) or failed to find successful transferability between models extrapolated into new regions ($AUC < 0.60$) (Gray et al. 2009; Wenger and Olden 2012). The variability and relevance amongst the environmental predictors is the primary reason transferability efforts fail (Fielding and Haworth 1995; Guay et al. 2003; Zharikov et al. 2007; Gray et al. 2009; Sundblad et al.

2009; Wenger and Olden 2012). As mentioned in the Introduction, widespread species that have greater dispersal capabilities and utilize more resources across a landscape may be less transferable than resource-limited species (Vanreusel et al. 2007). This means it is difficult to discern unsuitable and suitable habitats for generalist species. Intermediate species or species with only moderate specialization may be best suited for generation of models that can be widely applied across regions or times. (Dobrowski et al. 2011). Ultimately the factors that will most likely increase model transferability are lower model complexity, less correlation amongst variables, and a higher relevance of ecological predictors to habitat quality and alterations (Mac Nally 2000; Guisan and Thuiller 2005; Randin et al. 2006; Vanreusel et al. 2007; Zharikov et al. 2007; Peterson et al. 2007; Tuanmu et al. 2011; Wenger and Olden 2012). The variable success of these studies emphasizes the continued importance of evaluating model transferability in a variety of ecosystems and spatial scales amongst an array of taxa.

As habitats become altered due to anthropogenic change, it is important to assess how species distributions may shift through space and time. Predictive models can be powerful tools for forecasting species occurrences in poorly documented areas, selecting sites for species reintroduction and preservation, predicting species responses to environmental changes (Fielding and Haworth 1995), and reducing uncertainties associated with change. Few studies have evaluated relationships of species and environments well beyond the areas where training data were collected (Fielding and Haworth 1995; Rodríguez and Andren 1999; Morris et al. 2001; Whittingham et al. 2003). This is important because independent model transferability should be assessed

when there is an interest in making inferences outside the data used for fitting (Wenger and Olden 2012). The ability to use general models when making conservation decisions is particularly useful on larger scales. More statewide cooperation, regionally standardized protocols, and better regional datasets could greatly enhance the ability to more effectively assess model transferability. In regions that are particularly susceptible to land-use and climate impacts predictive models can have important management implications, but the impact of such models will be stronger when transferability has been robustly assessed.

Table 2.1 Model selection of clapper rail abundance models in South Carolina and Georgia.

State	Model Name	ΔAIC_c	ω_i	K	Loglikelihood	Beta Estimates \pm SE
South Carolina	distance to forest * elevation	0	1	6	-2174	1.51 ± 0.17 ; -1.32 ± 1.75
South Carolina	total landscape variable model (additive)	20.42	3.7E-05	10	-2167	NA
Georgia	distance to forest * proportion of brackish marsh	0	1	6	-2146	-0.94 ± 0.12 ; -0.30 ± 0.11
Georgia	total landscape variable model (additive)	50.98	8.5E-12	10	-2167	NA

Notes: Our total landscape variable model was an additive model including all predictor variables measured in our study (Table 2). Our top detection covariate for all models was the presence or absence of wind. AIC_c : ΔAIC_c for the i th model is computed as $AIC_i - \min(AIC)$, ω_i is the AIC model weight, K is the number of parameters, beta estimates explain the relationship of the parameter and clapper rail abundance, only significant relationships are reported.

Table 2.2 Mean and standard error values of our predictor variables used for analyses in each state.

Environmental Variable	SC mean \pm (SE)	GA mean \pm (SE)
Proportion of brackish marsh	11.67 \pm 2.60	43.47 \pm 3.30
Distance to forest (m)	450.77 \pm 42.09	644.64 \pm 36.89
Elevation (m)	0.32 \pm 0.034	0.29 \pm 0.0048
Distance to development (m)	2510 \pm 219.09	2011 \pm 106.37
Edge density	86.49 \pm 3.41	82.01 \pm 2.11
Patch area (ha)	738.37 \pm 73.80	910.85 \pm 40.08
Percent of marsh landscape	50.49 \pm 1.97	59.13 \pm 1.057

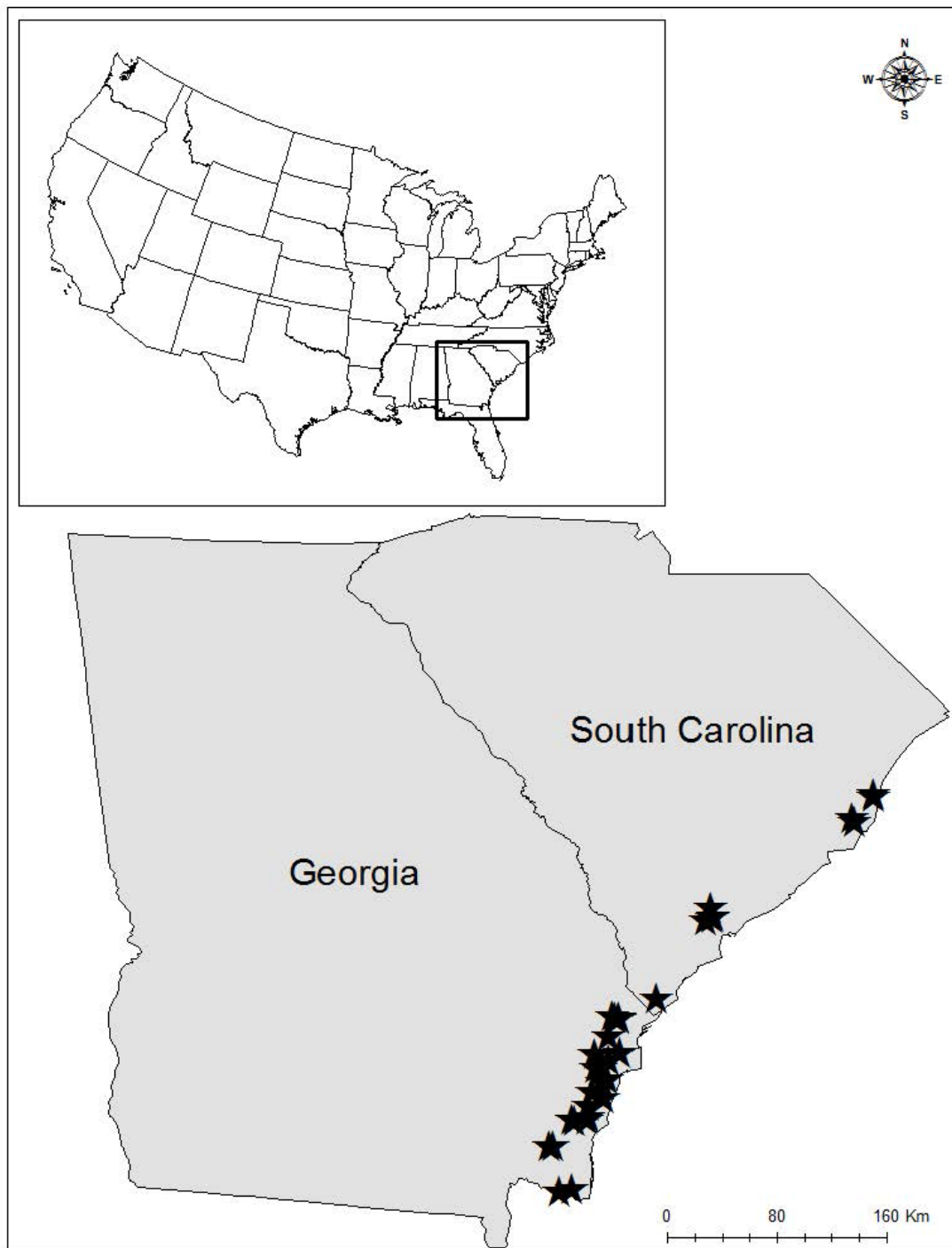


Figure 2.1 Map of survey transects (each transect contains 9 survey points) for the 2013 and 2014 field seasons in South Carolina and Georgia.

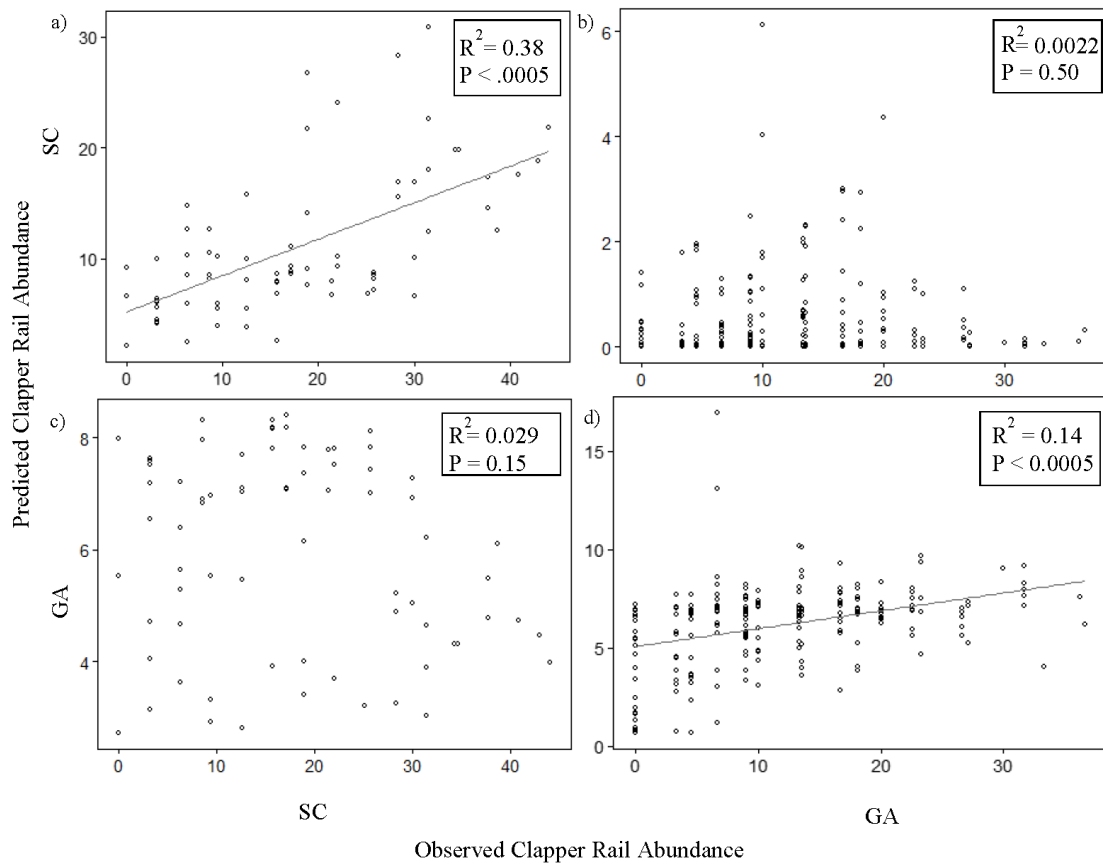


Figure 2.2 Comparison of observed and predicted top model parameter estimates in: a) South Carolina estimate the abundance of clapper rails in South Carolina b) South Carolina estimate the abundance in Georgia c) Georgia estimate the abundance in South Carolina d) Georgia estimate the abundance of clapper rails in Georgia.

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