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Marsh bird occupancy along the shoreline-to-forest gradient as marshes migrate from rising sea level

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Abstract. One mechanism by which coastal marshes may persist as sea-level rises is to expand landward into existing forest, a process known as marsh migration. Though recent studies highlight the importance of marsh migration to the conservation of birds associated with coastal marshes, marsh bird responses to this transition from forest to marsh are poorly understood. To address this need, we conducted surveys of five focal marsh bird taxa at 92 points distributed across the gradient from the shoreline to the marsh–forest interface in one of the most vulnerable regions to sea-level rise in North America where marshes have been migrating landward for at least several decades. Given this landward movement of the forest–marsh interface, we modeled focal taxa occurrence as a function of distance-to-forest, thereby assuming that marshes closer to the forest were newer than those closer to the shoreline. In addition, we investigated the effects of vegetation conditions and fire frequency. Occupancy probability of marsh birds decreased closer to the forest–marsh interface where woody vegetation was taller and herbaceous cover was dominated by *Cladium jamaicense*, suggesting migrated marsh may provide limited habitat for these bird species, at least in the short term. Though parameter estimate uncertainty for black rail (*Laterallus jamaicensis*) was high due to a limited number of detections, occupancy of this species may increase with the conditions associated with migrated marsh, specifically greater *C. jamaicense* dominance and decreasing distance-to-forest. Clapper/king rail (*Rallus crepitans/elegans*) occupancy was greater at sites that had burned more frequently over the past decade, and occupancy of all focal taxa was greater in areas with vegetation conditions consistent with the effects of fire in coastal marshes, including reduced herbaceous vegetation density and shorter woody vegetation. As such, prescribed fire may serve as an effective method of facilitating marsh migration and increasing the quality and quantity of habitat for coastal marsh birds as sea-level rises.

Key words: coastal wetland; disturbance; fire; inundation; marsh migration; occupancy; salinization.

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INTRODUCTION

Coastal marshes support a unique community of birds and have a disproportionate bird conservation value (Greenberg et al. 2006). However, the extent of coastal marshes has declined in recent decades as a result of habitat loss and degradation, much of which resulted from coastal development, invasive plants, altered hydrology, and coastal erosion (Takekawa et al. 2006, Silliman et al. 2009, Thorne et al. 2012). In the coming decades, rising sea level could add to these threats and amplify coastal marsh losses (Kennish 2001, Crosby et al. 2016).

Coastal marsh birds are expected to be negatively impacted by the accelerated rise in sea

level associated with anthropogenic climate change (Erwin et al. 2006, Woodrey et al. 2012, Hunter et al. 2015). Even a small rise in sea level could impact marsh habitat quality via increased vulnerability of nests to flooding, shifts in vegetation composition and structure, decreased food availability, and increased predation (Silliman et al. 2005, Erwin et al. 2006, Rush et al. 2009, Nuse et al. 2015, Hunter et al. 2016*b*). Changing hydrological conditions associated with saltwater intrusion, flooding, and rising sea level can have important implications for marsh composition and long-term persistence (Howes et al. 2010). Moreover, these conditions resulting from sea-level rise likely will interact with other stressors, including herbivory, fire, and drought (McKee et al. 2004, Silliman et al. 2005). Hence, the expected increase in frequency and severity of weather events such as storms and droughts has the potential to result in drastic changes in coastal marshes (Michener et al. 1997, Emanuel 2005, Howes et al. 2010).

Despite these threats to coastal marshes, there are two primary ways by which coastal marshes may persist as sea-level rises. In tidal systems fed by sediment-laden rivers, tidal flooding can regularly supply marshes with additional sediment that accretes over time, effectively allowing the marsh surface to keep pace with the rising sea level (Kirwan and Megonigal 2013). Additionally, inundation during storm events can deposit sediments in marshes and contribute to the vertical accretion of the marsh surface (McKee and Cherry 2009). In combination with continually expanding root mats of marsh vegetation, this vertical accretion can allow marshes to rise along with sea level and avoid permanent inundation and conversion to open water (Kirwan et al. 2016*a*). However, in marshes where sediment transport is low, tidal range is minimal, or sea-level rise is rapid, vertical accretion may not keep pace with sea-level rise (Voss et al. 2013, Crosby et al. 2016). In such systems, marsh persistence may depend on the second mechanism, marsh migration, which refers to the gradual shift of marsh communities landward, replacing existing vegetation communities such as forest or freshwater wetland (Kirwan et al. 2016*b*, Schieder et al. 2018). As with vertical accretion, the potential for marsh migration varies across marshes. Coastal squeeze between the eroding shoreline and existing human infrastructure or land uses can prohibit the landward movement of marshes (Doody 2004). Similarly, the resistance of mature trees to saltwater exposure can limit the pace of marsh migration relative to rising sea level, resulting in net marsh loss (Field et al. 2016). More complex mechanisms, such as interaction with other disturbances like fire, may also play a role in marsh migration, but these processes are not well understood (Poulter et al. 2009).

Fire may be an especially important disturbance mechanism in coastal wetlands because of its potential to facilitate marsh migration and create habitat conditions required by marsh birds (Frost 1995, Rogers et al. 2013). The tolerance of mature trees to acute saltwater exposure can slow the rate of forest decline as sea-level rises (Field et al. 2016). However, salt stress may decrease the likelihood an individual tree may survive a fire, resulting in increased fire severity in areas recently exposed to saltwater (Niinemets 2010). Moreover, seedlings and saplings have a lower tolerance to salinity than mature trees, so regeneration of tree species in the wake of fire may be limited, allowing marsh grasses to encroach into previously forested areas (Poulter et al. 2009). In marsh systems, fire consumes accumulated dead vegetation which can improve foraging conditions for birds that walk along the marsh surface, such as rails (Conway et al. 2010, Rogers et al. 2013, Morris et al. 2017). As such, fire may help to increase both habitat quality and quantity for coastal marsh birds, particularly those associated with the upper marsh edges, in the context of rising sea level.

Despite the essential role of marsh migration for many coastal marshes in the face of rising sea level, little is known about how marsh birds will respond to this process. The structure and composition of recently created marshes that have migrated into areas that were previously forest, or migrated marshes, may differ from older marshes, for example, by having persisting live or dead woody vegetation. The rate at which migrated marshes become suitable for marsh birds may lag behind coastal erosion or increased inundation, resulting in a net loss of marsh bird habitat (Field et al. 2016). Moreover, marsh migration may benefit different species to different degrees, depending on the characteristics of the migrated marsh and the habitat associations of a given species. For example, marsh birds

susceptible to flooding may use the upper marsh edge, or high marsh, whereas other species may use the wetter and often more saline low marsh environments (Wilson et al. 2007, Van De Pol et al. 2010, Thorne et al. 2015). The responses of marsh birds to changing marsh conditions thus have important implications for the conservation of these species as sea level continues to rise and marsh migration becomes more widespread.

Several previous studies used simulation models to predict hypothetical marsh bird responses to rising sea level (Rush et al. 2009, Nuse et al. 2015, Hunter et al. 2016*b*). Potentially because of the slow rate of marsh migration, forecasting analyses project greater losses for high marsh environments compared to low marsh (Thorne et al. 2015). If marshes become increasingly comprised of low marsh conditions, marsh birds normally associated with high marsh conditions may become more exposed to stressors such as flooding (Van De Pol et al. 2010, Hunter et al. 2016*a*). Therefore, marsh migration may be particularly important for birds that are high marsh specialists. However, more studies documenting observed marsh bird responses as marshes migrate are needed to complement predictive forecasts.

To this end, we aimed to investigate patterns in marsh bird use in one of the most vulnerable areas to rising sea level in North America (Hauer et al. 2016). We modeled occurrence of six focal marsh bird species as a function of distance-to-forest and vegetation characteristics across a gradient from the shoreline to the retreating forest edge. In addition, we incorporated the 15-yr fire history, because fire is thought to be a driver of marsh migration (Poulter et al. 2009) and marsh bird habitat quality (Conway et al. 2010, Austin and Buhl 2013, Rogers et al. 2013). As such, our results will help to direct future efforts to facilitate marsh migration and conserve coastal marsh birds in the context of rising sea level.

Methods

Study area

The Albemarle-Pamlico Peninsula (APP) in eastern North Carolina is comprised of approximately 50% wetlands, over 20,000 ha of which are herbaceous marshes of varying salinity (Moorhead and Brinson 1995). This variation in salinity is partially caused by a chain of barrier islands that limit water exchange between the sounds and the ocean to a few inlets. The Albemarle Sound, bordering the APP to the north, has no inlets to the ocean, and salinity stays below 5 ppt most years (Manda et al. 2014). In contrast, the Pamlico Sound to the south has more exchange with the ocean, but near-shore salinity remains substantially lower than seawater, typically between 8 and 15 ppt (Buzzelli et al. 2003). This geomorphology of the APP also results in low astronomical tidal height. Instead, water movement is primarily wind-driven (Manda et al. 2014). The resulting limited flooding frequency, coupled with low allochthonous sediment delivery from rivers, results in slow vertical accretion rates for the coastal wetlands of the APP, which are not expected to keep pace with even a moderate increase in sea-level rise (Moorhead and Brinson 1995).

Unlike other salt marshes occurring in the southeastern United States, *Spartina alterniflora* was rare in our study area, likely because of lower maximum salinity. On the APP, marshes closer to the shoreline and with greater salinity are comprised predominately of *Juncus romerianus*, but other common marsh plants in these environments include *Disticlis spicta* and *Spartina patens*. Traveling landward from the shoreline, *J. romerianus* is gradually replaced by *Cladium jamaicense*, which predominates in the high marsh zone. Freshwater marshes comprised of *Typha* spp. also were present in the study area, but to a lesser extent than brackish marshes.

Over the past century, widespread land cover change has been observed at coastal forested sites on the APP, likely due to a combination of rising sea level, fire, and other disturbances (Poulter 2005). Rates of lateral retreat of the forest–marsh interface varied across sites, but Poulter (2005) estimated rates higher than 1 m/yr between the 1930s and the 1990s. Comparable estimates have been reported for similar large estuary systems in eastern North America, such as the Chesapeake Bay (Schieder et al. 2018). Given this lateral retreat of the forest–marsh interface, we assume that marshes closer to this interface are younger than those closer to the shoreline.

Site selection

We identified candidate marshes to survey for marsh birds using a combination of aerial photography and the National Wetlands Inventory

(USFWS 2010). At all marshes to which we were granted access, we further limited our scope to areas accessible within 30-min walking from a road, or 60-min paddling a canoe from a launch site. Within these accessible areas, we randomly selected 127 points across the gradient from the shoreline to the forest edge with a minimum between-point distance of 400 m. We excluded 35 of the 127 original points that were located in forest conditions with dense woody vegetation and little herbaceous cover, despite being classified as marsh in the National Wetlands Inventory. Nonetheless, after excluding these points, the final sample of 92 points (Fig. 1) covered a gradient of woody vegetation cover.

Bird surveys

An observer conducted a 10-min, unlimited radius point-count at each point between one and three times in each of 2016 and 2017, for a total of two to six visits per point. In accordance with the Standardized North American Marsh Bird Monitoring Protocol, surveys were conducted during the window from 30 min prior to sunrise to 2 h after sunrise. Surveys were not conducted during rain or excessive wind. During the first 5 min of the 10-min point-count, the observer recorded the detection/non-detection of six focal species: black rail (*Laterallus jamaicensis*), Virginia rail (*Rallus limicola*), clapper rail (*Rallus crepitans*), king rail (*Rallus elegans*), least bittern (*Ixobrychus exilis*), and seaside sparrow (*Ammodramus maritimus*). This procedure was repeated for the second 5 min of the 10-min point-count, but during this second 5-min period a recording of vocalizing marsh birds was broadcast to elicit responses from focal species. We acknowledge that use of playback may violate some of the underlying assumptions of the occupancy model we fit to our observations, such as the independence between adjacent sampling locations, but we spaced the sampling locations sufficiently far

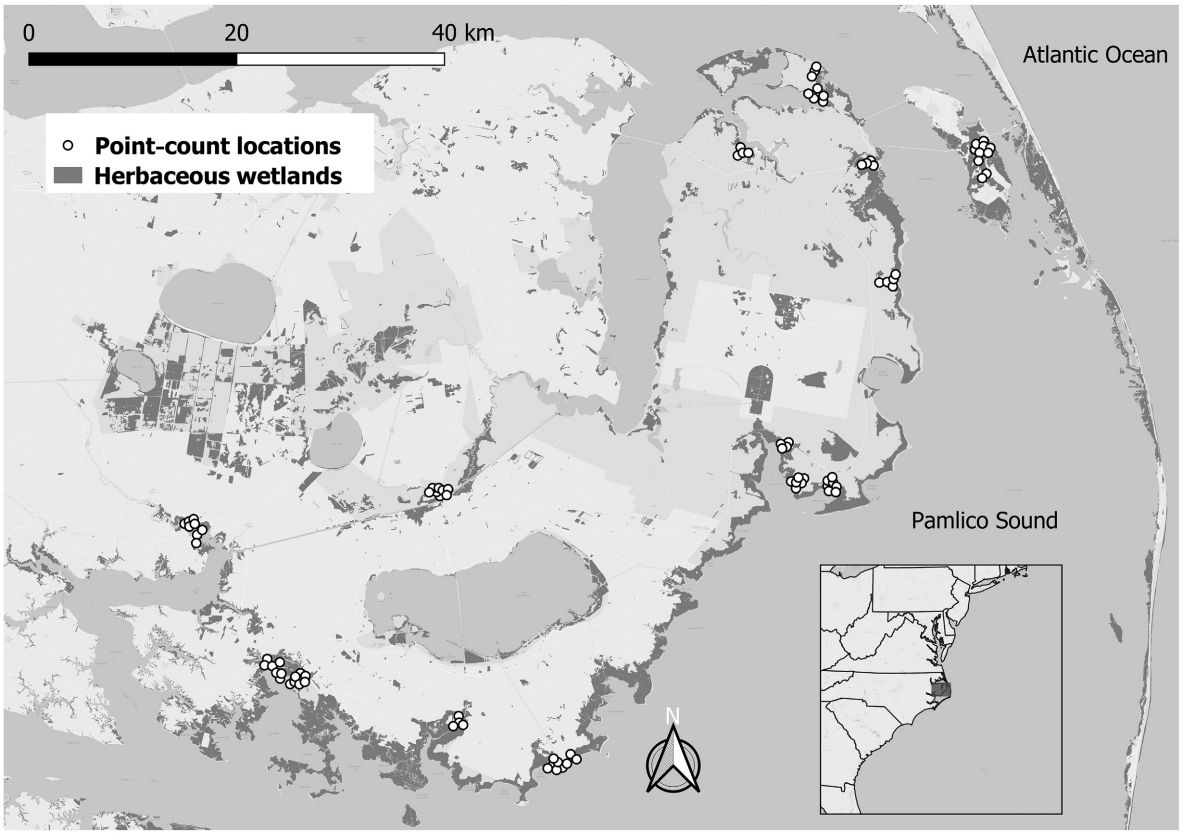


Fig. 1. Marsh birds were surveyed in coastal marshes of eastern North Carolina at 92 point-count locations in 2016 and 2017.

from each other to minimize the likelihood of drawing in individuals from another sampling location. We used the recording from the Saltmarsh Habitat & Avian Research Program in Region 9, which includes black rail, Virginia rail, least bittern, king rail, and clapper rail. We did not include the vocalization of common gallinule (*Gallinula galeata*), as we primarily were interested in species associated with herbaceous cover. Additionally, we did not use playback for seaside sparrows nor did we record the detection/non-detection for this species in 2016.

Because the black rail is nocturnal and difficult to detect, we supplemented the above survey protocol with additional sampling using autonomous recording units (ARU). We deployed two SM4 ARUs from Wildlife Acoustics at a random sample of 23 of the 92 point-count locations for between one and three nights between 1 April and 30 June 2017. The ARU was set to record all sound from 2 h before sunset to 2 h after sunrise on the nights they were deployed. We analyzed the recordings using Kaleidoscope acoustic analysis software to identify black rail vocalizations (see Bobay et al. 2018, for a more detailed description of acoustic analysis).

Habitat variables

We measured habitat variables that we expected to best reflect the variability between older marshes near the shoreline and newer marshes near the forest edge. To measure the vertical structure of marsh vegetation, we used a 1.27 cm diameter PVC pole cut to 1.5 m in length and marked into 0.1-m sections. Along a random compass bearing away from the point-count location, we placed the pole vertically every 10 m out to 100 m, for a total 10 pole surveys per point, per visit (Moorman and Guynn 2001, Taillie et al. 2015). For each pole survey, we recorded the number of 0.1-m pole segments (hereafter: hits) that came in contact with herbaceous vegetation. In addition, we recorded the maximum height of woody vegetation within 2 m of the pole, using the pole to measure the height to the nearest 0.1 m. We repeated this procedure on each successive visit to a given point, but along a new random compass bearing. We averaged the number of hits across the total number of pole surveys to obtain one value of vegetation density within 100 m of the point-count location. For woody vegetation height, we averaged across only the number of pole surveys where woody vegetation was present, to obtain an average height of the woody vegetation within 100 m of the point-count location. Because woody vegetation can be sparse in herbaceous marshes, this approach to averaging was meant to minimize the impact of pole surveys that did not have woody vegetation present, despite woody vegetation being present within 100 m of the point-count location.

We quantified marsh species composition according to the dominant marsh plant species, *C. jamaicense* and *J. romerianus*, within 2 m of each pole survey. Because marsh plants tend to grow clonally and in patches, determining the dominant species within 2 m of the pole was straightforward. We calculated an average for each point-count location by summing the number of pole surveys at a point-count location where each species was dominant, and divided by the total number of pole surveys at that point-count location. As such, these quantities approximated the dominance of a given marsh plant species within 100 m of the point-count location.

Lastly, we calculated the fire history and distance to the forest edge for each point-count location. To calculate fire history, we used fire perimeters for all prescribed fires and wildfires occurring between 2000 and 2017 (MTBS 2018). We summed the number of fires containing a given point-count location to represent the fire history for that point. For the distance to the forest edge, we first differentiated between marsh and forest using a 12-m resolution map of mean vegetation height derived from Light Detection and Ranging (LiDAR) data collected in 2014 (L. S. Smart, *unpublished data*). We considered any cell with a mean vegetation height >3 m as forest. When comparing the LiDAR-derived vegetation map to aerial photographs and field observations, delineating at the 3-m threshold best matched the point at which living trees occurred.

Analysis

We used single-season, single-species occupancy models to relate detections of Virginia rail, clapper/king rails, black rail, least bittern, and seaside sparrow to habitat covariates, while accounting for imperfect detection. Clapper and king rails were considered together because these

two species are extremely difficult to differentiate by vocalizations normally, and in this region, they are known to co-occur at many sites and can also hybridize (Perkins et al. 2009, Maley and Brumfield 2013). We modeled occurrence of each focal taxon using the single-species, single-season occupancy model described by MacKenzie et al. (2002). Our general approach was to fit a global model for each taxon (Eqs. 1 and 2) using the *occu* function in the R package Unmarked (Fiske and Chandler 2011) and fit successive models of all possible combinations of the covariates using the dredge function in the R package MuMIn (Bartón 2018). We then calculated model-averaged parameter estimates of all models with an Akaike's information criterion (AIC) within 2 of the top-ranked model (i.e., that with the lowest AIC). Specifically, we used the full averages where averaged parameter values include models in which the covariate is not included by assuming the parameter estimate = 0 for those models (Burnham and Anderson 2002).

The global model for each taxon included three covariates on detection and seven covariates on occupancy. We included both linear and quadratic effects of time of day and date of year of visit $j = 1,2, \ldots J$ to point-count location $i = 1,2, \ldots M$ as covariates on detection probability (p_{ij}), where J = the total number of repeated visits and M = the total number of sites (Eq. 1). The third detection covariate was type, which was an indicator variable corresponding to the two portions of the point-count: the first 5 min without playback, and the second 5 min with playback (Taillie et al. 2015, Cherukuri et al. 2018). We included herbaceous vegetation density, woody vegetation height, dominance of *C. jamaicense* within 100 m, dominance of *J. romerianus* within 100 m, distance-to-forest, and number of fires since 2000 at point-count location i as covariates on occupancy probability (ψ_i) for a given focal taxon (Eq. 2). To account for variation between the 2 yr of sampling, we included an effect of year, which we forced into every model of the dredge.

$$\begin{aligned}\text{logit}(p_i) = {} & \alpha_0 + (\alpha_1 \times \text{Time}_{ij}) + (\alpha_2 \times \text{Date}_{ij}) \\ & + (\alpha_3 \times \text{Time}_{ij}^2) + (\alpha_4 \times \text{Date}_{ij}^2) \\ & + (\alpha_5 \times \text{Type}_{ij})\end{aligned} \quad (1)$$

$$\begin{aligned}\text{logit}(\psi_i) \sim {} & \beta_0 + (\beta_1 \times \text{Herb_hits}_i) \\ & + (\beta_2 \times \text{Woody_height}_i) \\ & + (\beta_3 \times \textit{Cladium}_i) + (\beta_4 \times \textit{Juncus}_i) \\ & + (\beta_5 \times \text{Dist_to_for}_i) \\ & + (\beta_6 \times \text{Num_fires}_i) + (\beta_7 \times \text{Year}_i)\end{aligned} \quad (2)$$

Because we had a limited number of observations for black rail, we were unable to fit the global model or other models with many parameters. Instead, we fit univariate models for each occupancy covariate of interest. In addition to the covariate of interest, we included survey type (with an additional category for ARU-based survey) as a covariate on detection in all models, and year as a covariate on occupancy.

To summarize the combined effects of four covariates we believed best reflected the differences between older and newer marshes, we used the model-averaged parameter estimates to predict occupancy across the gradient from forest to marsh. Specifically, we assumed that distance-to-forest and *J. romerianus* dominance decreased linearly from the shore to the forest edge, whereas woody vegetation height and *C. jamaicense* dominance increased linearly from the shore to the forest edge. We examined correlation between distance-to-forest and vegetation metrics to support these assumptions by calculating Pearson's correlation coefficients for all covariates. We then predicted the occupancy probability for each focal taxon, excluding black rail, across the range of each of these variables that we observed in the study (Table 1).

Table 1. Minimum, mean, and maximum values of continuous covariates used to model occupancy of marsh birds in coastal marshes of eastern North Carolina (2016 and 2017).

Site covariate	Minimum	Mean	Maximum
Distance-to-forest (m)	0.0	197.9	723.2
Juncus dominance (%)	0.0	3.2	100
Herbaceous density (no. of hits)	1.6	7.2	12.9
Woody height (m)	0.0	0.4	2.2
Number of fires	0	0.8	5
Cladium dominance (%)	0.0	2.6	100

Results

We observed low correlation ($-0.4 < \rho < 0.4$) among occupancy covariates, except for moderate correlation between *J. romerianus* and *C. jamaicense* dominance ($\rho = -0.49$). Near the forest edge, woody vegetation height and dominance of *C. jamaicense* were greater, reflected by negative correlation coefficients between distance-to-forest and these two variables ($\rho = -0.24$ and -0.32, respectively). In contrast, as distance-to-forest increased, *J. romerianus* dominance increased. We observed low correlation ($\rho = -0.03$) between herbaceous vegetation density and distance-to-forest.

We observed substantial variation in both detection and occupancy among marsh bird taxa. Clapper/king rail was the most widespread taxon with a mean occupancy probability of 0.84 (Table 2). Black rail was the rarest taxon with an occupancy probability of 0.17; however, inclusion of sampling using ARUs increased the occupancy probability of black rail to 0.38 (Table 2). The inclusion of ARUs only increased the probability of detecting a black rail from 0.05 to 0.08, but it more than doubled the number of sites at which black rail was detected to 11 (Table 2).

The occupancy probability for four focal taxa (black rail excluded because we used a different modeling approach for this species) was near 0 at the upper end of the shoreline-to-forest gradient. However, the occupancy probability for least bittern was low (<0.3) across the range of all variables we considered (Fig. 2). Both Virginia rail and clapper/king rail had a probability of occupancy slightly >0 at the upper end of the shoreline-to-forest gradient (Fig. 2). Though occupancy probability for Virginia rail was high closer to shoreline, this species showed the weakest response to the shoreline-to-forest gradient. Similarly, seaside sparrow and clapper/king rail were most likely to occupy marsh sites closer to the shoreline (Fig. 2). For seaside sparrow, this response was driven by a positive relationship between occupancy and distance-to-forest, whereas this response for clapper/king rail was driven by a positive relationship with dominance of *J. romerianus* (Table 3).

Vegetation structure and species composition appeared to be important drivers of occupancy

Table 2. The number of sites at which each focal marsh bird species was detected (naïve occupancy), the average detection probability (p), and the average occupancy probability (ψ) in coastal marshes of eastern North Carolina (2016–2017).

Species	Code	Sites detected	Mean detection	Mean occupancy
Seaside sparrow	SESP	35	0.87	0.37
Clapper/king rail	CLRA	72	0.61	0.84
Least bittern	LEBI	26	0.34	0.24
Virginia rail	VIRA	57	0.34	0.49
Black rail	BLRA	4	0.05	0.17
Black rail w/ ARU†	BLRA	11	0.08	0.38

† Including detection data derived from autonomous recording units (ARU).

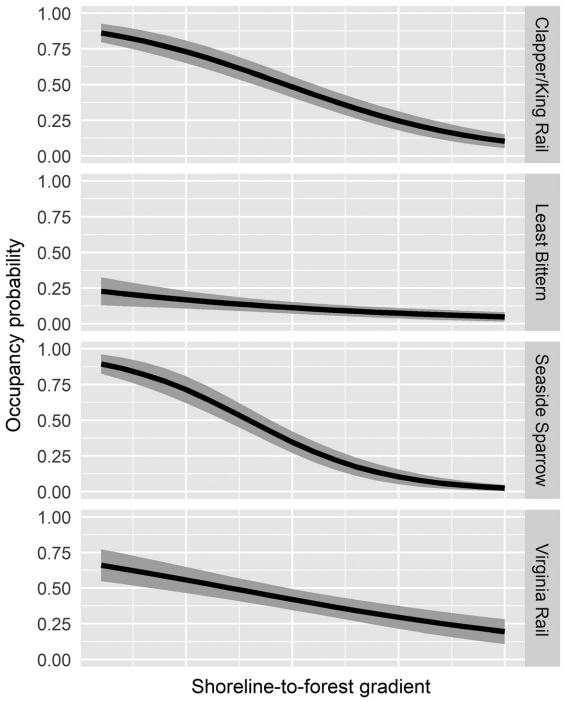


Fig. 2. Occupancy probability for clapper/king rail, least bittern, seaside sparrow, and Virginia rail predicted using model-averaged parameter estimates of four variables that were assumed to reflect the gradient from the shoreline to the forest edge: distance-to-forest, *Juncus romerianus* dominance, *Cladium jamaicense* dominance, and woody vegetation height. Shaded regions represent 95% confidence intervals. Occupancy was not predicted for black rail because we did not detect enough individuals to fit the model with all covariates related to the shoreline-to-forest gradient.

Table 3. Model-averaged parameter estimates (with 95% confidence intervals in parentheses) derived from all models within <2 AIC of the top-ranked model for covariates on occupancy of focal marsh bird species (SESP, seaside sparrow; CLRA/KIRA, clapper/king rail; LEBI, least bittern; VIRA, Virginia rail; and BLRA, black rail) in coastal marshes of eastern North Carolina (2016 and 2017).

Covariate	SESP	CLRA/KIRA	LEBI	VIRA	BLRA
Dist to forest	0.66 (0.12, 1.2)	–	–	–	−0.38 (−1.25, 0.49)
Juncus	1.05 (0.51, 1.59)	1.18 (0.68, 1.68)	–	1.04 (0.47, 1.60)	−0.01 (−1.05, 1.03)
Year	–	−1.83 (−2.79, −0.87)	−1.09 (−2.08, −0.11)	−0.37 (−1.18, 0.45)	1.11 (−0.99, 3.21)
Herbaceous hits	–	−0.66 (−1.15, −0.17)	–	−0.90 (−1.42, −0.37)	−0.23 (−1.14, 0.67)
Woody height	–	–	−0.53 (−1.12, 0.05)	−0.39 (−0.84, 0.05)	0.002 (−0.80, 0.80)
Fires	–	0.73 (0.24, 1.21)	–	–	19.8 (−175.2, 214.8)
Cladium	–	–	–	0.73 (0.19, 1.27)	0.56 (−0.36, 1.48)

Notes: AIC, Akaike's information criterion. Missing values (–) represent variables that were not present in any of the models within <2 AIC of the top-ranked model. Due to limited observations, we were unable to fit the whole suite of models for black rail, so parameter estimates reported for this species were derived from models with only year and the parameter of interest as covariates on occupancy.

for all focal taxa. Specifically, occupancy of seaside sparrow, clapper/king rail, and Virginia rail increased with increasing dominance of *J. romerianus*. Virginia rail also increased with increasing dominance of *C. jamaicense*. Despite high uncertainty in parameter estimates for black rail, we observed a weak relationship between occupancy and increasing *C. jamaicense* dominance for this species. Occupancy probabilities for least bittern and Virginia rail may have declined with increasing woody vegetation height, though the 95% confidence intervals for both of these parameters slightly overlapped zero (Table 3). Occupancy of rails consistently declined with increasing herbaceous vegetation density. Clapper/king rail was the only taxon for which we observed a response to fire frequency and was more likely to occupy sites that burned more frequently in the past decade (Table 3).

Discussion

The low occupancy probability for marsh birds at the upper end of the shoreline-to-forest gradient suggests habitat quality of newly migrated marshes is lower than older marshes. Though migrated marsh apparently offers little value to seaside sparrow, they may benefit from marsh migration indirectly, given the positive response to distance-to-forest observed in this study, as well as previous studies (Rush et al. 2009, Hunter et al. 2016*a*). Virginia rail, one of the more generalist of the suite of marsh birds we studied, appeared to be the most likely to use migrated marsh compared to other marsh birds, given their positive association with *C. jamaicense* dominance, which was greater in marshes closer to forest. Indeed, we observed Virginia rail using marshes with evidence of a fairly recent (~10 yr) transition from forest, such as standing dead trees. Though we did not detect enough black rail to make robust inferences about their habitat associations, the places where we did detect black rail support observations from previous studies (Wilson et al. 2007) that suggest that marsh environments near the forest edge are important for this species because of its susceptibility to high water and flooding.

Prescribed fire could serve as a useful tool for facilitating marsh migration and creating higher quality habitat for marsh birds as sea-level rises. Though we only observed strong evidence for an effect of fire frequency for clapper/king rails, other species may benefit as well, given responses to habitat characteristics typically associated with post-fire environments (Mitchell et al. 2006). For example, Virginia rail occupancy was greater in areas with less dense herbaceous vegetation and shorter woody vegetation, both conditions present soon after prescribed fire (Mitchell et al. 2006). Moreover, several previous studies have documented increases in occupancy of marsh birds following prescribed fire (Conway et al. 2010, Rogers et al. 2013). Facilitating marsh migration would likely come at the cost of habitat loss for forest-associated wildlife, but the current rate of habitat loss for these species due to sea-level rise is likely limited (P. J. Taillie et al.,

unpublished manuscript). Granted, the application of fire at these transitions from forest to coastal marsh is complicated by several logistical challenges. Wet, unconsolidated soil may require special equipment for moving personnel and installing fire breaks. Additionally, dense woody vegetation and deep, organic soils could present significant risk of unintentionally severe fires (Mitchell et al. 2014). Nonetheless, on large, public properties with the adequate resources, prescribed fire could prove to be an effective tool for coastal marsh bird habitat management.

The elusive nature of some marsh bird species continues to present challenges for monitoring. Despite regular historical observations of black rail in the study area, the small number of observations limited our ability to make meaningful statistical inferences about occupancy of this species. In addition, the very low estimated detection probability could result in artificially high estimates of occupancy for this species. Least bittern was both rare and elusive, though not to the extent of black rail, which may explain the lack of relationship between least bittern occupancy and the habitat variables we considered. It is also possible that variables we did not consider may better explain variation in least bittern occupancy, for example, proximity to open water patches for catching fish. Though king and clapper rails are more common, our detections of these species were almost exclusively aural, precluding observers from accurately discerning species. The differences in habitat related to salinity for these two species (Maley and Brumfield 2013) could result in disparate responses to rising sea level that we were not able to detect. These rare and elusive marsh bird species likely will require more coordinated long-term monitoring across larger spatial extents to better understand how they will respond to rising sea level and marsh migration. In addition, future studies should investigate spatial and temporal patterns of habitat use in more detail, for example, by tracking individuals through time.

In addition to the stressors responsible for previous declines of marsh birds, rising sea level could dramatically influence the quality and quantity of habitat for these birds. Given that sea level is expected to rise at an accelerated rate in response to anthropogenic climate change, the future for coastal marsh birds remains highly uncertain. In addition to monitoring both how marshes are changing and how marsh birds respond to those changes, developing novel management strategies, such as facilitated marsh migration, that consider future conditions likely will be necessary.

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