DETERMINING THE STATUS AND DISTRIBUTION

OF THE EASTERN BLACK RAIL

(*LATERALLUS JAMAICENSIS*)

IN COASTAL TEXAS

by

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ABSTRACT

The black rail (*Laterallus jamaicensis*) is a small and secretive marsh bird that inhabits coastal high marshes and freshwater wetlands throughout the Americas and is a species of conservation concern. In Texas, winter migrant and breeding populations of the eastern black rail (*L. j. jamaicensis*) are known to occur in disjunct wetlands along the Gulf Coast. Black rail distribution and life history, however, are poorly studied in Texas. I studied the spatial ecology and habitat requirements of black rails in marshes of the Texas Gulf Coast from 2015 to 2018. Through the application of occupancy models, radio telemetry, capture-recapture studies, and a geographic information system, I provide an evaluation of factors that influence the distribution of black rails at multiple spatial scales in coastal Texas. Using occupancy data, I developed a species distribution model for the black rail in coastal Texas to identify important areas for the bird on a landscape-scale. I found positive associations between black rail occurrence and average annual precipitation as well as herbaceous vegetation density. High-marsh habitats with minimal tidal influence containing >50% herbaceous vegetative cover, especially gulf cordgrass (*Spartina spartinae)*, had the highest predicted occupancy probabilities. Using radio telemetry, I tracked individual black rails during winter to estimate home range size and examine habitat associations at the home-range scale. Home range size of wintering black rails in Texas was somewhat smaller than estimates of those during breeding in Florida, which represents the only other published home range study for the subspecies. Habitat selection within black rail home ranges were similar to occupancy model findings: black rails selected high-marsh habitats with vegetation types that included large amounts of gulf cordgrass and avoided the low tidal marsh. Home ranges also contained an elevational gradient which may allow for rails to seek higher ground during times of increased water levels. I also looked at effects of disturbance from prescribed fire within black rail habitats. Prescribed fire is a common method used to manage the

coastal marshes inhabited by black rails. Results from capture studies conducted in multiple burn plots indicated black rails will use habitats within a wide range of burn regimes (27 - 76 months post-burn). I found no strong relationships between black rail density and habitat features measured in study plots. Nevertheless, there might be a minimum cover requirement in that I only detected black rails ≥27 months post-burn. For the closely related yellow rail (*Coturnicops novaboracensis*), plots with lower herbaceous density were favored more. Yellow rails will also use habitats within a wide range of burn regimes (11 – 84 months post-burn) and may require a shorter return interval post-burn before using the habitat. There was no correlation between months post-burn and density of either species of rail which might be explained by a lack of correlation between herbaceous density and months post-burn. Management of burn regimes for black rails and yellow rails in coastal Texas should maintain a mosaic of seral stages. My studies provide information that is crucial for beginning to understand black rail distribution in coastal Texas as well as for managing habitat for the species.

CHAPTER 1

GENERAL INTRODUCTION

Wetlands are among the world's most important ecosystems as they play pivotal roles in carbon sequestration, improve water quality, provide flood control, and are huge sources of biological diversity and ecosystem benefits [1,2]. There are several different wetland types that are found in a range of hydrologic conditions and vary in size, location, and anthropogenic influence. Wetlands usually occur at the interface of terrestrial (such as forests and uplands) and aquatic (such as lakes and oceans) systems and can be divided into two major groups: inland and coastal [3]. Inland wetlands include peatland, freshwater marsh and swamp, and riparian ecosystems, and coastal include mangrove wetlands, tidal salt marsh, and tidal freshwater marsh [3]. Freshwater wetlands cover only 1% of the earth's surface yet support >40% of the world's species (Ramsar Convention Bureau 2001). Nevertheless, wetland loss and degradation is extensive. Factors that have led to wetland loss and degradation include alteration and filling for agriculture and development, subsidence and fragmentation due to petroleum exploration and development, and pollution from commercial, residential and agricultural contaminants [3]. Coastal wetlands are under the additional threat of sea-level rise resulting from global climate change [4]. Organisms that inhabit wetlands are uniquely adapted to persist in these ecosystems and many inhabit these wetlands throughout their annual life cycle. As these habitats are lost or degraded, many of the vertebrate species endemic to wetlands are increasingly being listed as species of conservation concern, threatened, or endangered.

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Some estimate that about 50% of wetlands have been lost worldwide due to anthropogenic activities and those that remain are degraded due to hydrological alterations, eutrophication, sedimentation, salinization, filling, and exotic species invasions [5]. Many coastal wetlands that were once expansive and uninterrupted have suffered from anthropogenic development and fragmentation, e.g. levees, dams, irrigation canals[6]. Wetlands typically occur as small, isolated patches interspersed within a matrix of upland habitat. Likewise, many local populations of wetland species are also small and isolated, thus vulnerable to extinction [7]. An estimated 46 percent of federally threatened or endangered species are wetland obligates [8]. Loss and fragmentation of wetlands may have numerous effects on the vertebrate species inhabitants. For example, some wetland-obligate avian species including some grebes, bitterns, rails, and shorebirds may be more likely to occur in large versus small wetland areas, especially birds considered to be habitat specialists [9-12].

Marsh birds inhabit emergent wetlands and many are deemed "secretive" since they live and generally move within dense vegetation, vocalize infrequently, and thus are difficult to detect [13]. Many species of marsh birds are experiencing population declines, including all 10 members of family Rallidae found in North America [14-17]. In addition to habitat loss, the major threats to these species are accumulation of contaminants in wetland substrates e.g. mercury [18], and invasive plant species altering trophic function and outcompeting native plants [19,20]. To conserve marsh birds, there needs to be a comprehensive understanding of their abundance, population trends, spatial distributions, and the resources required throughout their life cycle.

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The enigmatic black rail (*Laterallus jamaicensis*) is a stealthy, deftly elusive little bird and is likely one the most secretive marsh birds in North America. According to the Eastern Black Rail Conservation & Management Working Group, the eastern black rail (*L. j. jamaicensis*) may be "the most endangered bird species along the Atlantic and Gulf coasts of North America". Some estimates indicate a 75% or greater decline in population sizes over the past 10-20 years [21]. The eastern black rail is listed as endangered in six eastern states and has been proposed to be listed as "threatened" by the U.S. Fish and Wildlife Service. In Texas, research is sparse even though black rails were first documented in the state as far back as 1879 [22]. Furthermore, based on the amount of marsh habitat in the state, Texas may have an abundance of eastern black rails. Thus, Texas represents a knowledge gap that is a critical component for assessing the status of the subspecies. Determining the status of a species or its populations is an arduous task but there are some principles that can help inform conservation efforts: resiliency and redundancy. In simple terms, population size can be thought of as a measure of resiliency and the number of populations as a measure of redundancy. However, long-term survival of a species depends upon the amount of perturbations *i.e.* stochastic events, predation, or hunting pressure they experience in relation to the number and size of its populations. The objective of this research was to provide much needed data required to determine the distribution and thus the potential redundancy of the eastern black rail in coastal Texas.

Population Size and Abundance

Some of the most fundamental questions in ecology relate to the abundance of organisms and how abundance changes in time and space. Population in the broad sense

refers to a collection of individuals of a species in a defined area. Estimating population size by counting all individuals present at a given time and location may be possible if the species is easy to detect, i.e. large and somewhat slow moving in relation to the observer, but this is rarely the case and for something like a secretive marsh bird, this method is not feasible whatsoever. Abundance estimates, simply put, are population estimates that account for counting errors and can be obtained by sampling a subset of the population of interest. Distribution size as well as trend in distribution size are important determinants of extinction risk, however abundance and trends in abundance are most frequently used to assess conservation priorities [23]. Species with small populations showing negative trends are assigned a higher conservation priority (e.g. federally listed, International Union for Conservation of Nature Red List of Threatened Species). Additionally, abundance is potentially a more sensitive measurement of future change than extent of distribution since population declines may occur before a reduction in distribution is observed [24].

Patterns of species distribution and abundance are ultimately determined by the underlying dynamics of a population. There are two fundamental parts to studying population dynamics: 1) measuring population abundance, and 2) understanding the drivers of population change. These drivers can be thought of as inputs and outputs, i.e. fluctuations in births/deaths and immigration/emigration. The impacts that inputs and outputs have on population dynamics can be estimated by examining the interactions and relationships between them and density-dependent and density-independent factors. It is likely that marsh birds that are not colonial are primarily affected by density-independent

factors such as seasonal phenology of food supply, prolonged drought or rain, predators, loss of habitat, etc. As abundance of birds in an area increases and all optimal habitat becomes occupied, individuals would then be affected by density-dependent processes such as having to compete for nesting sites, food or territorial space [25].

Species Distributions

The extent to which a species occupies a region is correlated to the abundance of that species. There tends to be a positive relationship between the number of sites in which a species occurs regionally and its local abundance [26]. Whether species naturally occupy large areas or have small, restricted distributions is largely dependent upon their dispersal capabilities, life history and habitat requirements. Population size, geographic range, and habitat suitability influence commonness and rarity of species. A species may be considered rare because it has low population densities, or a limited range. For widespread and rare species alike, local population densities tend to gradually decline from the interior of the species' geographic range to the boundaries [26,27]. Though in some circumstances and for reasons such as competitive exclusion, predator-prey interactions, or the physical environment, there can be abrupt boundaries that create precipitous declines in density [28,29]. One difference with respect to rare species is that they occupy a smaller proportion of sites within their range, including the middle, and are associated with more sampling error [26]. On a sufficiently small scale, population density should exhibit a multimodal distribution due to patchiness of suitable habitat, social interaction, or a combination of these factors [26]. While rarity may naturally occur, anthropogenic activities such as habitat destruction or alteration, overharvesting, or the introduction of

invasive species may also impose rarity. Anthropogenic activities are constantly altering

species distributions, thereby influencing rarity, by creating or destroying habitat,

barriers, and corridors, and even moving the species themselves, either by accident or on

purpose.

Resiliency and Redundancy

Conservation biology arose from the growing global concern about the loss of

ecosystems such as rainforests and coral reefs, as well as individual species of animals

and plants. It originated in population biology and community ecology. Usually, the main

focuses of species conservation are determining minimum viable populations and

minimum areas necessary for a species to persist, i.e. prevent extinction. Redford, et al. [30]

suggest that beyond the prevention of extinction, conservation should also include

ensuring populations are healthy, self-sustaining, genetically robust, and thus resilient to

environmental changes.

Shaffer and Stein [31] developed the population attributes termed "the three R's":

representation, resiliency, and redundancy. The principle of representation denotes the

importance of saving some of everything, everywhere. In other words, successful

conservation includes saving populations of each species in each of the different regions

or environments in which it occurs. Ecological resiliency was first introduced by Holling

[32] with the initial focus on resiliency of ecosystems, but since then the concept has

acquired several definitions [33-35]. Ecological resilience is often defined as the amount of

disturbance that a system can absorb and still persist in its current state [34]. Although this

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definition refers to system-level resiliency, resilience can be applied at smaller scales such as regional or local patch level [35,36].

Measuring resiliency requires determining the existence of thresholds that separate different stability domains (the regions within which population stability occurs) and how close a system is to those thresholds [32,35]. The best way to learn about thresholds is to cross them through experimental manipulation [37]. Since this may be exceedingly risky, a more conservative angle is to identify regime shifts and changes by examining long-term data on the variables that describe and govern the system and how a population responds to disturbance or stress. For example, long-term monitoring or monitoring that overlaps with an environmental perturbation can be used to estimate temporal variation in population size [38-40]. Additionally, evaluating other variables such as the biotic/abiotic factors that influence demography [41] can be used to examine the demographic processes that influence population change [42,43].

A species is comprised of populations distributed across a landscape and the more populations across the landscape, the greater the redundancy. The term metapopulation refers to a group of spatially separated subpopulations of the same species which interact at some level [44]. Size, structure, and connectivity of a metapopulation is likely to influence resilience [45,46]. Small, more isolated subpopulations are theoretically more likely prone to extinction due to demographic, environmental, and genetic stochasticity, and natural catastrophes [47-49]. A larger subpopulation should be more resilient than a smaller one, thus if two neighboring subpopulations fuse together, the abundance of the population increases thereby making it more resilient, but redundancy is reduced. It is

essential to conserve multiple populations of a species to maintain redundancy and genetic variability, and accordingly, a species is able to persist if enough populations exist. This prompts the question: how many populations are enough to prevent extinction? It is difficult to determine this "magic number", especially since different species have different extinction thresholds and many variables must be considered when assessing the population needs of a threatened species, especially specific threats to the species.

To count the number of populations across an area, there needs to be spatial boundaries between populations if they are to be considered separate. It is therefore important to understand what maintains those boundaries. Boundaries may be easily explained by the habitat, such as natural or manmade barriers, changes in permeability (ability to move between two adjacent areas) of the landscape matrix, or more obscure and complicated if due to dispersal behavior [50]. Additionally, birds can exhibit interspecific or intraspecific territoriality that can influence distribution within their habitat. Individuals that are territorial tend to be more regularly dispersed (as opposed to clumped) and they "defend" an area characterized as their "territory" [51]. The area defended by an individual may change in time and space depending upon sex, time of year, and possibly age [52]. A species "home range" would include those areas not defended that an individual uses during daily activities *i.e.* to search for food, that possibly overlap with neighboring individuals, thus home range is generally larger than territory [52]. The area included in both home range and territory may shift and change

during the life of an individual [52]. To properly manage a species, it is essential to understand how much living space individuals require.

This research seeks to provide data for the evaluation of resiliency and redundancy of the eastern black rail in Texas. I provide an evaluation of factors that influence the distribution of black rails at multiple spatial scales in coastal Texas. Chapter 1 briefly introduces the species and a complete literature review of both subspecies of black rail found in North America is provided in the Appendix. Chapters 2 - 4 focus on the research and methodology conducted for this dissertation. Specifically, a species distribution model (SDM) for the black rail in coastal Texas to aid in finding new populations and assess redundancy (Chapter 2), second, home range estimates and habitat selection to better understand the needs of the species in the region (Chapter 3), and lastly, resource selection in relation to management practices *i.e.* prescribed burn, to assess resiliency (Chapter 4).

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CHAPTER 2

SPECIES DISTRIBUTION MODEL FOR THE EASTERN BLACK RAIL IN

COASTAL TEXAS

Abstract

Knowledge of a species' distribution is essential for creating a conservation management plan. Predictive habitat models are valuable in the assessment of rare or cryptic species in vast landscapes such as the Texas coast. In this study, I developed a species distribution model using an occupancy modeling framework for the eastern black rail (*Laterallus jamaicensis*) in coastal Texas. I conducted repeated call play-back surveys in 2015 and 2016 and detected 286 black rails at 109 survey points. With this data, I modeled black rail occurrence while accounting for imperfect detection and mapped results using a geographic information system. There was a positive association between black rail occurrence and average annual precipitation, herbaceous vegetation density, the salty prairie vegetation type, and salt and brackish high tidal marsh vegetation, and fresh and intermediate tidal marsh vegetation. Habitats with minimal tidal influence containing >50% herbaceous vegetative cover, especially gulf cordgrass (*Spartina spartinae)*, had the highest predicted occupancy probabilities. These characteristics are consistent with what has been found in other regions of the country. Occupancy estimates were also higher in areas with higher average annual precipitation, which increases from west to east in Texas. My results indicate that black rails distribution in coastal Texas might be restricted by relatively high precipitation levels and dense herbaceous cover provided by cordgrasses.

Introduction

Species distribution models, also called ecological niche models, or species or climatic envelope models, are used to derive spatially explicit predictions of habitat suitability for a species. The creation of this type of model is accomplished by combining species occurrence or abundance data at known locations with environmental and spatial parameters at those locations [1]. Predictions can be made to identify new sites within the range of sites sampled (interpolation) and to novel, unsampled sites (extrapolation) across a landscape [1]. Projecting the generated functions to areas that have not been sampled but where the environmental characteristics are known is a cost-effective method of predicting suitable habitat for a species. Estimating suitable habitat for a species is critical for species conservation as suitable habitat that has not been sampled can be evaluated for species presence or if absent, to identify potential sites for species reintroduction.

The black rail (*Laterallus jamaicensis*) is the smallest member of family Rallidae found in North America and is often thought of as one of the most elusive birds on the continent. The small body size and particularly shy nature of this rail, coupled with occupying dense, marsh vegetation has made the species difficult to detect and study. Often compared in behavior to that of a mouse[2,3], black rails are very reluctant to fly and more inclined to flee on foot when disturbed, usually remaining completely unseen under dense marsh vegetation. Black rails are usually confined to moist soil marshes or those with the shallowest (fresh or salt) water. The narrow habitat characteristics and cryptic behavior of this rail makes it difficult to detect requiring well-planned aural surveys to conduct a population assessment [4,5]. Species distribution models (SDMs) can be

particularly useful in determining the distribution of hard to detect species such as the black rail. By predicting suitable areas with high probability of occupancy, refuge managers can eliminate surveying sites with low probability of presence and focus efforts to areas with suitable habitat, thereby increasing efficiency in locating birds.

Different methods for modeling species distributions. There are many different methods available to generate SDMs and the results can be general or specific. A general species envelope can be developed using basic climate variables such as precipitation and temperature, but by including vegetation and land-cover data, it is possible to produce a specific, habitat-based distribution. In other words, the quality and interpretation of the results of an SDM is dependent upon the data inputs. There are four types of species data typically used in building SDMs: presence-only, presence-background, presence-absence, and occupancy-detection [6,7]. The robustness of these methods and the quantities that they can estimate occur in a hierarchy as described below [6].

Often, the only data available about a species occurrence is presence-only (PO), which is simply a record of the species at a location with no information on survey methods, and information on absences are unknown or inadequate. The most commonly used PO data are museum records which usually contain geographical coordinates of the sites where the species was found [8]. There are a few issues associated with using PO data, one being sample selection bias where some areas in a landscape are surveyed more intensely than others, usually areas that are more convenient to sample [9,10]. Another issue is that the proportion of occupied sites, or prevalence of the species, cannot be determined with PO data since absence data is unavailable [9]. Also, PO data typically do not contain

information on sampling area and search time, which is relevant for mobile animals that may wander and thus presence or absence is associated with a spatial and/or temporal scale[9,11]. Additionally, PO methods produce limited inference because habitat preference of a species might vary with habitat availability [6].

Presence-background (PB) data is similar to PO data except they contain information on environmental characteristics of the wider landscape [7]. Methods using PB data estimate habitat preferences of a species by comparing the habitat characteristics at sites where the species was present, with habitat characteristics throughout the region being modeled (or the "background"). Some drawbacks of using PB data are the same as those listed above for PO data, there is a lack of information on absence data and sampling effort. PB and PO data are commonly modeled using MaxEnt [12] or regression methods [13].

Presence-absence (PA) data inform on whether a species was detected or not at a set of sampled sites and usually include information about sampling effort. Since absence data is available, estimation of prevalence is possible. This allows the differentiation of whether a species is rare and well-surveyed or common but under-surveyed [6]. Models using this type of data are less susceptible to sample selection bias because in some circumstances, bias associated with presence and absence records are similar and the biases cancel each other out [9]. Because the survey method used to obtain PA data is often known, the temporal and spatial scale is known as well. Modeling methods using PA data compare environmental characteristics at sites where the species was detected with those sites where it was not to estimate the probability of observing a species at a given

location. Common modeling methods include generalized linear models (GLMs) and generalized additive models (GAMs) [14,15].

Occupancy-detection (DET) data are similar to PA data but are more robust in that they enable models to account for imperfect detection by including a detection probability parameter when estimating occupancy. Since DET data are collected via repeated visits, it is possible to obtain a detection probability, an estimate of the probability of detecting a species if it is present at a site [16]. Not accounting for detectability can lead to underestimated probability of occurrence and over- or underestimation of habitat suitability [6,17]. DET data can be modeled hierarchically using a logistic regression to describe the distribution of the species and relate the probability of its presence at a site to environmental predictors through a logit link function [7].

Imperfect detection. Failing to detect a species at a location does not guarantee that the species is absent. A fundamental complication with species occurrence data is that species are often detected imperfectly [18]. Treating observed species occurrence and distribution as the actual or true occurrence and distribution without accounting for imperfect detection can lead to poorly formulated SDMs and reduce their predictive accuracy [19,20]. Further, failure to account for imperfect detection can lead to biased estimates of habitat relationships and possibly incorrect inference [19,21].There are two types of errors that can be made when collecting species occurrence data: false-negative errors (claim the species is absent when it is actually present) and false-positive errors (claim the species is present when in fact it is absent). False-negatives are more likely in a cryptic species like black rails where presence is usually indicated only if a bird calls

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during an aural survey [19]. Additionally, the detection probability of occupancy can be influenced by sampling methods and effort, habitat characteristics, and environmental variables such as wind speed, lunar phase, and temperature [22,23]. Taking all these factors into account, underestimation of occupancy for rare and cryptic species such as black rails would probably be common if imperfect detection is not accommodated.

Coastal Texas might be a stronghold for the eastern black rail, yet an SDM is lacking. Along the Atlantic coast, eastern black rails are experiencing dramatic declines [24]. Previous studies have focused on determining habitat requirements on a highly localized scale via home range and territory studies [25-27], and using occupancy modeling to determine important occupancy covariates [28-30]. No study thus far has used habitat requirements and occupancy data to map habitat suitability. In this study, I collected detection data in an occupancy framework to develop an SDM for the black rail along the Texas coast.

Methods

Study area. The study area consisted of multiple refuges within the Gulf Prairie and Marshes ecoregion [31] along the Texas coast (Figure 2-1). This region is a fairly level, slow-draining plain intersected by rivers and streams that drain into the Gulf of Mexico. This region occupies about 3,844,500 ha, is less than 46 m in elevation, and includes tidal flats, dunes, bays and estuaries surrounded by salt grass marshes, remnant tallgrass prairies, scattered oak parklands and mottes, and tall woodlands in the river bottomlands [31]. Areas in which I conducted this study consisted of densely vegetated herbaceous

marshes dominated by graminoids such as cordgrasses (*Spartina* spp.), interspersed with

forbs such as sea oxeye daisy (*Borrichia frutescens*), and with minimal woody cover.

Figure 2-1 Study sites along Texas Gulf Coast where black rail (*Laterallus jamaicensis*) call play-back surveys were conducted March-May 2015-16.

The sites where call-playback surveys were conducted include Anahuac National

Wildlife Refuge (13,759 ha) in Chambers County, Brazoria NWR (17,973 ha) in Brazoria

County, San Bernard NWR (21,853 ha) in Brazoria and Matagorda Counties, Mad Island

Wildlife Management Area (2,913 ha), Clive Runnells Family Mad Island Marsh

Preserve (2,858 ha) in Matagorda County, and Powderhorn Ranch (6,981 ha) in Calhoun

County. The two refuges located at Mad Island were considered to be one site and

hereafter will be referred to as the Mad Islands. These sites represent a gradient of climatic conditions as they occur along an annual precipitation gradient with the highest precipitation (~145 cm/year) at Anahuac NWR and lowest (~106 cm/year) at Powderhorn Ranch [32]. Additionally, temperatures along the Texas coast increase from northeast (32˚C max and 5˚C min) to southwest (33˚C max and 7˚C min)[32].

Species occurrence data. Using GIS layers of the study sites, transects were established along roads and firebreaks that ran through potential and unsuitable habitat and then a subset was randomly selected. Survey points were spaced 400 m apart to avoid risk of double counting individual birds and to increase total area surveyed. Surveys were conducted twice a day: 30 minutes prior to sunrise until 2 hours after sunrise, and 2 hours prior to sunset until 30 minutes after sunset. Observers recorded the number of black and clapper rails (*Rallus crepitans*) to respond to call-playback, as well as direction of each bird using a compass and an estimate of the distance of each bird within distance bands (0-50 m, 50-100 m, 100-150 m, >100 m). Clapper rail calls were included since a previous study found an increase in response of some marsh birds with the broadcast of a heterospecific's call [33]. Numerous environmental covariates were recorded during each survey including temperature, wind speed, time of day, lunar phase, ambient noise level, and disturbance (i.e. cattle grazing or recently burned). Call play-back surveys were conducted up to six times per survey point following the general methodology described by Conway [4]. The survey sequence was slightly modified as follows: four minutes of passive listening followed by 30 seconds of black rail calls, then 30 seconds of silence followed by 30 seconds of clapper rail calls, and then a final 30 seconds of silence. Calls

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on mp3s were obtained to reflect the regional dialect. Sound pressure in the broadcast speakers was measured at 80-90 db and the surveyor stood at least 2 m away from the speaker. Surveys were conducted March-May 2015-16.

Detectability and occupancy. Tolliver, et al. [23] estimated habitat relationships with black rail occupancy and abundance at the scale of the study site using the same survey data as my study. I used lunar phase and wind speed as detection covariates in my occupancy models since Tolliver, et al. [23] reported that these were the only influential environmental covariates. Lunar phase was coded as a discrete variable that ranged from 0 (no moon) to 15 (full moon) [22]. I analyzed the same data set as Tolliver, et al. [23]. Because I did not use the vegetation survey data as a habitat covariate in the occupancy analysis, I was able to analyze data from 348 of the survey points, whereas Tolliver, et al. [23] removed survey points with missing vegetation surveys ($n = 308$).

Based upon the species' life-history information, I modeled black rail occupancy as a function of habitat covariates potentially affecting presence-absence of the species [16]. The covariates included the following: vegetation type (from The Ecological Mapping Systems of Texas), existing vegetation cover (EVC), marsh type (salt, intermediate-brackish, or fresh), soil slope gradient, soil drainage class, percent emergent wetland, distance to open water, and annual precipitation (30-year normals, 1981-2010). Vegetation type was a categorical variable parsed into four categories. Three of the categories were the vegetation types with adequate proportions of black rail detections necessary to calculate reliable occupancy estimates and avoiding convergence issues (Table 2-1). Those three vegetation types were Gulf Coast: Salty Prairie, Coastal: Salt

and Brackish High Tidal Marsh, and Chenier Plain: Fresh and Intermediate Tidal Marsh (see Table 2-2 for partial vegetation type descriptions).

I evaluated the predictive performance of the top model using the receiver operating characteristic (ROC) and the area under the curve (AUC) technique. The ROC-AUC analysis is commonly used to visualize the performance of a binary classifier and is created by plotting the true-positive rate against the false-positive rate [41,42]. The AUC ranges in values from 0 to 1.0, where a model with all incorrect predictions has an AUC of 0, an AUC of 0.5 is where the true- and false-positives are equal, and an AUC of 1.0 represents perfect classification (all positives and negatives are true). For the ROC-AUC analysis, I fit a logistic regression model to a training data set (random 50% of data, $n = 174$) and then assessed it by applying the model to an evaluation data set (the other half of the data, $n = 174$). I also extracted predicted occupancy estimates at plotted estimated locations of black rail detections to visually assess model performance.

The fourth vegetation category constituted all other vegetation types grouped together. EVC represents the vertically projected percent cover of the live canopy layer for a 30-m grid cell. The EVC data was also categorical which I converted to a continuous scale of 0 to 9, with 1 representing the lowest cover category 10 – 20% herbaceous cover, 9 representing the highest 90 – 100% herbaceous cover, and 0 representing a cover category other than herbaceous (e.g. tree cover). Soil slope gradient influences the rate at which runoff flows and erodes the soil surface and is the difference in elevation between two points, expressed as a percentage where 0-2% is nearly level and >35% is very steep. Soil drainage classes represent the moisture condition of the soil

throughout the year in its natural condition and can range from "very poorly drained" to "excessively drained". Percent emergent wetland was obtained by calculating the proportion of pixels categorized as a type of emergent wetland within 100 m^2 buffered area around survey points. Annual average precipitation ranged from 103.1 - 143.9 cm among study sites.

Table 2-1 Number of surveys conducted within each vegetation type and number of black rail detections within each vegetation type from the Ecological Mapping System of Texas [34].

Vegetation type (MoRAP Code)	Surveys conducted	Black rails detected
Gulf Coast: Salty Prairie (2207)	125	46
Chenier Plain: Fresh and Intermediate Tidal Marsh (5807)	70	24
Coastal: Salt and Brackish High Tidal Marsh (5617)	55	22
Coastal: Salt and Brackish Low Tidal Marsh (5607)	20	4
Columbia Bottomlands: Grassland (4707)	19	2
Coastal and Sandsheet: Dune and Coastal Grassland (6307)	14	0
Native Invasive: Baccharis Shrubland (9116)	8	1
Coastal and Sandsheet: Deep Sand Live Oak Shrubland (6405)	8	0
Non-native Invasive: Chinese Tallow Forest, Woodland, and Shrubland (9214)	5	0
Coastal and Sandsheet: Deep Sand Live Oak Forest and Woodland (6402)	4	0
Chenier Plain: Salt and Brackish High Tidal Marsh (5717)	3	1
Row Crops (9307)	3	0
Urban Low Intensity (9411)	3	0
Columbia Bottomlands: Hardwood Forest and Woodland (4704)	2	0
Open water (9600)	2	0
Gulf Coast: Salty Shrubland (2206)	1	1
Columbia Bottomlands: Live Oak Forest and Woodland (4702)	1	0
Columbia Bottomlands: Evergreen Shrubland (4705)	1	0
Columbia Bottomlands: Herbaceous Wetlands (4717)	1	0
Coastal: Tidal Flat (5600)	1	0
Coastal: Salt and Brackish High Tidal Shrub Wetland (5616)	1	0
Coastal and Sandsheet: Deep Sand Live Oak Swale Marsh (6407)	1	0
Total:	348	101

Table 2-2 Descriptions (partial) from Elliott [35] of vegetation types used as habitat covariates in occupancy models.

Vegetation type	Description
Gulf Coast: Salty Prairie (MoRAP code: 2207)	Saline soils, generally near-coast. Sites may be nearly monotypic stands of *Spartina spartinae* (Gulf cordgrass). Forbs are generally uncommon but may include *Borrichia frutescens* (sea ox-eye daisy). Shrubby species may invade the prairie, commonly including *Iva frutescens* (shrubby sumpweed).
Coastal: Salt and Brackish High Tidal Marsh (MoRAP code: 5617)	Irregularly flooded marsh dominated by graminoids such as *Spartina patens* (marshhay cordgrass), *Distichlis spicata* (saltgrass), and *Schoenoplectus* spp. (bulrushes). Some irregularly flooded sites may become shrub-dominated with species such as *Iva frutescens* (shrubby sumpweed) or *Baccharis halimifolia* (eastern baccharis).
Chenier Plain: Fresh and Intermediate Tidal Marsh (MoRAP code: 5807)	Herbaceous system, mucky soils, salinity <4ppt. Dominants are graminoids and woody cover is minor but may include *Iva frutescens* (bigleaf sumpweed) or *Baccharis halimifolia* (baccharis).

I obtained GIS data on vegetation type from The Ecological Mapping Systems of Texas (Texas Parks & Wildlife Department and Water Development Board, https://tpwd.texas.gov/gis/programs/landscape-ecology/supporting-documents, accessed June 2018), EVC data from LANDFIRE: LANDFIRE Existing Vegetation Type layer (http://landfire.cr.usgs.gov/viewer/, product name: LF 2014 LF 1.4.0, accessed Aug 2018), soil slope and soil drainage data from United States Department of Agriculture, Natural Resources Conservation Service (http://datagateway.nrcs.usda.gov/, accessed Sept 2018), emergent wetland and open water data from U. S. Fish and Wildlife Service (http://www.fws.gov/wetlands/, accessed Aug 2018), marsh type from U.S. Geological

Survey Wetland and Aquatic Research Center

(https://pubs.er.usgs.gov/publication/sir20175044, accessed Aug 2018), and annual

precipitation data was obtained from PRISM Climate Group, Oregon State University

(http://prism.oregonstate.edu, accessed July 2018).

To obtain values most representative of the area around a survey point, I used the

Spatial Analyst tool in ArcGIS 10.6 (ESRI, Redlands, CA) to calculate focal statistics for

the soil data, EVC, and vegetation type variables. This analysis calculates the majority

(value that occurs most often) of the cells in the specified neighborhood around it.

Vegetation type at estimated locations of survey points where black rails were detected

were ground-truthed using data from the vegetation surveys conducted at each survey

point and Google Earth. At survey points were black rails were detected, focal statistics

were calculated at estimated distance-sampled points. All continuous covariates were

standardized to have a mean of 0 and a standard deviation of 1.0 before analysis [36].

The program R [37] was used for all statistical analyses. To determine which of the

occupancy covariates were influential, I first estimated multi-seasonal occupancy models

for each candidate covariate. Multi-seasonal occupancy models were estimated because

data was collected in two consecutive years. I considered covariates influential if they

were statistically significant at an 85% ($|Z| \geq 1.41$, $P \leq 0.15$) confidence level [38]. With the

occupancy covariates deemed as influential, I conducted a two-year analysis of

occupancy dynamics using the *colext* function in the R-package 'unmarked' [39]. I fitted

multi-season occupancy models with increasing complexity holding colonization, and

extinction parameters constant, and used Akaike's information criterion adjusted for

small sample size (AIC$_C$) for model selection. Models with ΔAIC$_c$ values $\leq$2 were considered to have strong support [40]. I used the *predict* function in 'unmarked' to obtain predictions of occupancy which I then used to produce maps of areas with suitable habitat.

I evaluated the predictive performance of the top model using the receiver operating characteristic (ROC) and the area under the curve (AUC) technique. The ROC-AUC analysis is commonly used to visualize the performance of a binary classifier and is created by plotting the true-positive rate against the false-positive rate [41,42]. The AUC ranges in values from 0 to 1.0, where a model with all incorrect predictions has an AUC of 0, an AUC of 0.5 is where the true- and false-positives are equal, and an AUC of 1.0 represents perfect classification (all positives and negatives are true). For the ROC-AUC analysis, I fit a logistic regression model to a training data set (random 50% of data, $n = 174$) and then assessed it by applying the model to an evaluation data set (the other half of the data, $n = 174$). I also extracted predicted occupancy estimates at plotted estimated locations of black rail detections to visually assess model performance.

Results

Over the two years of surveys combined, a total of 3,899 surveys were conducted at 375 individual survey points. I detected 286 individual black rails at 109 points during 225 of the surveys (Table 2-3). Across all study sites, naïve occupancy (not accounting for detection) was 0.20 in 2015 and 0.18 in 2016 [23]. Three transects comprising 27 points

were only surveyed the second year and thus were excluded from the multi-season

occupancy analysis.

Table 2-3 Results from black rail (*Laterallus jamaicensis*) call play-back surveys conducted at 375 survey points at five sites along the Texas Gulf coast, March-May 2015-16.

Site	Total # surveys conducted	Individual black rails detected	Individual survey with detection	Points surveyed with detections
Anahuac NWR (105 survey points)	1042	141	108	42 (40%)
Brazoria NWR (80 survey points)	911	53	43	27 (34%)
San Bernard NWR (65 survey points)	683	64	47	21 (32%)
Mad Islands (84 survey points)	845	27	28	19 (23%)
Powderhorn Ranch (41 survey points)	418	0	0	0
Total (375 survey points)	3899	285	225	109 (29%)

Occupancy covariates determined to be influential from preliminary analysis, and

thus used in the model selection, were vegetation type, EVC, marsh type, precipitation,

and soil slope. The summed weights for each occupancy covariate across all models, and

thus relative importance of each covariate, were: vegetation type = 1.0, EVC = 0.74,

marsh type = 0.20, precipitation = 1.0, and soil slope = 0.34. The model selection analysis

showed the model with vegetation type, EVC, and precipitation as the top model (Table

2-4). There was one competing model (ΔAIC_c <2) which included the same predictors as

the top model and soil slope, however I selected the top model since the 85% CI of the

soil slope coefficient overlapped zero (85% CI = -0.24 – 0.66). The combination of

vegetation type, EVC, and precipitation with the highest $\hat{\psi}$ (0.87, ±0.07) was Gulf Coast:

Salty Prairie, plus EVC: herbaceous cover 70 – 80%, and average annual precipitation

between 140-145 cm (Figure 2-2).

Table 2-4 Candidate models explaining black rail (*Laterallus jamaicensis*) occurrence in the coastal region of Texas from 2015 to 2016. Models accounted for imperfect detection. *K* is the number of parameters in the model, AIC_c is Akaike's Information Criterion adjusted for small sample size, ΔAIC_c is the difference in AIC_c value relative to the top model, and w_i is the AIC_c weight.

Model[a]	K	ΔAICc	w_i	Deviance	R^2
$\hat{\psi}$ (Vegetation type+ EVC + precipitation)	11	0.00	0.40	326.66	0.20
$\hat{\psi}$ (Vegetation type + EVC + precipitation + soil slope)	12	1.49	0.19	326.53	0.20
$\hat{\psi}$ (Vegetation type + precipitation)	10	2.14	0.14	327.69	0.19
$\hat{\psi}$ (Vegetation type + EVC + marsh type + precipitation)	15	3.10	0.09	325.43	0.21
$\hat{\psi}$ (Vegetation type + precipitation + soil slope)	11	3.35	0.08	327.49	0.19
$\hat{\psi}$ (Global)	16	4.08	0.05	325.18	0.21
$\hat{\psi}$ (Vegetation type + marsh type + precipitation)	14	5.59	0.03	326.55	0.20
$\hat{\psi}$ (Vegetation type + marsh type + precipitation + soil slope)	15	6.22	0.02	326.21	0.20
$\hat{\psi}$ (Vegetation type + EVC + marsh type)	14	9.31	0.00	327.48	0.19
$\hat{\psi}$ (Vegetation type + EVC + marsh type + soil slope)	15	11.09	0.00	327.43	0.19
$\hat{\psi}$ (Vegetation type + marsh type)	13	12.92	0.00	328.89	0.18
$\hat{\psi}$ (Vegetation type + marsh type + soil slope)	14	14.70	0.00	328.83	0.18
$\hat{\psi}$ (Vegetation type + EVC)	10	17.47	0.00	331.52	0.15
$\hat{\psi}$ (Vegetation type + EVC + soil slope)	11	19.04	0.00	331.42	0.15

$\widehat{\Psi}$ (Vegetation type)	9	22.16	0.00	333.20	0.13
$\widehat{\Psi}$ (Vegetation type + soil slope)	10	23.56	0.00	333.05	0.14
$\widehat{\Psi}$ (EVC + precipitation)	8	40.00	0.00	338.16	0.08
$\widehat{\Psi}$ (Precipitation + soil slope)	8	40.00	0.00	338.16	0.08
$\widehat{\Psi}$ (EVC + marsh type)	11	41.23	0.00	336.96	0.09
$\widehat{\Psi}$ (Marsh type + soil slope)	11	41.23	0.00	336.96	0.09
$\widehat{\Psi}$ (EVC + precipitation + soil slope)	9	41.80	0.00	338.10	0.08
$\widehat{\Psi}$ (EVC + marsh type + precipitation)	12	41.98	0.00	336.65	0.10
$\widehat{\Psi}$ (EVC + marsh type + soil slope)	12	43.23	0.00	336.96	0.09
$\widehat{\Psi}$ (EVC + marsh type + precipitation + soil slope)	13	43.59	0.00	336.55	0.10
$\widehat{\Psi}$ (EVC)	7	47.52	0.00	340.54	0.06
$\widehat{\Psi}$ (EVC + soil slope)	8	47.70	0.00	340.08	0.06
$\widehat{\Psi}$ (Precipitation)	7	48.23	0.00	340.71	0.05
$\widehat{\Psi}$ (Marsh type + precipitation)	11	50.75	0.00	339.34	0.07
$\widehat{\Psi}$ (Marsh type + precipitation + soil slope)	12	52.36	0.00	339.25	0.07
$\widehat{\Psi}$ (Marsh type)	10	53.77	0.00	340.60	0.06
$\widehat{\Psi}$ (Soil slope)	7	62.16	0.00	344.20	0.01
$\widehat{\Psi}$ (Intercept only)	6	64.95	0.00	345.39	0.00

[a]Base model for all models included $\widehat{p}$ (wind speed + lunar phase), where $\widehat{p}$ denotes detection probability.
EVC = existing vegetation percent cover.
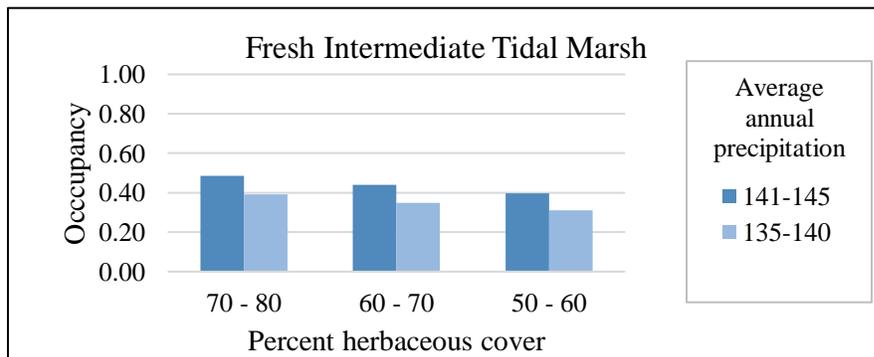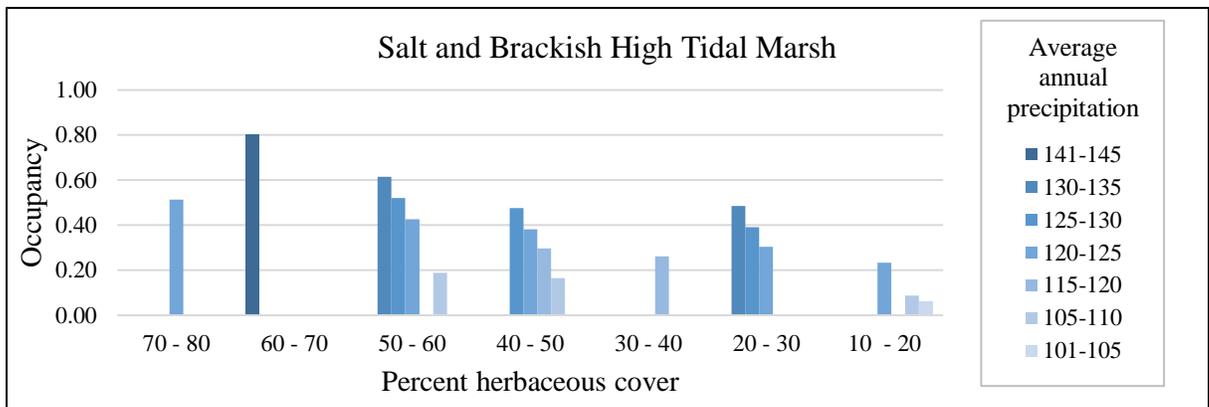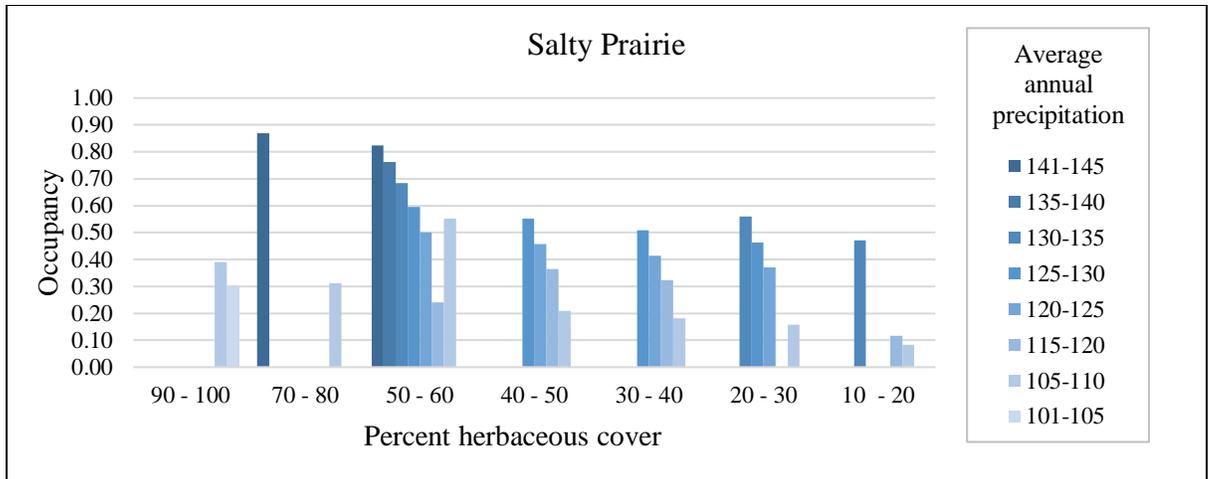
Figure 2-2 Predicted probabilities of black rail (*Laterallus jamaicensis*) occupancy ($\hat{\psi}$) for combinations of percent herbaceous cover and average annual precipitation (cm) within three different vegetation types along the coastal region of Texas. The absence of a value for $\hat{\psi}$ within a percent herbaceous cover category indicates the combination of vegetation type, percent herbaceous cover, and/or precipitation did not occur within the areas surveyed.

Occupancy was influenced positively by EVC, precipitation, and by all three vegetation types besides "other", which was the reference category (Table 2-5). As was also reported in Tolliver, et al. [23], detection was negatively influenced by wind speed and positively influenced by lunar cycle, where detection probability increased under low wind conditions closer to a full moon (Table 2-5). A very low proportion of the study region was predicted to have habitat suitable for black rails (Figure 2-3 and Table 2-6). The study site with the greatest proportion of the best predicted habitat ($\hat{\psi} \geq 40\%$) relative to its size was Anahuac NWR (51.1%), whereas Powderhorn Ranch had the least (8.7%). The study site with the largest amount of predicted habitat of the highest suitability was Anahuac NWR, whereas Powderhorn Ranch had the smallest amount (Table 2-7). The AUC of the ROC was 0.67, indicating that the model correctly discriminated between black rail presence and absence ~67% of the time. Extraction of occupancy predictions at estimated locations showed that 71% of the detections were in habitat with an occupancy estimate of $\geq 40\%$.

Table 2-5 Untransformed regression coefficients for the covariates from the selected multi-season occupancy model potentially affecting site occupancy ($\hat{\psi}$) and detection probabilities ($\hat{p}$) of black rails (*Laterallus jamaicensis*) in coastal Texas in 2015 and 2016.

Covariate	$\hat{\beta}$	SE	*P*-value
$\hat{\psi}$ intercept	-4.47	1.06	<0.001
Gulf Coast: Salty Prairie	4.43	1.11	<0.001
Coastal: Salt and Brackish High Tidal Marsh	4.13	1.12	<0.001
Chenier Plain: Fresh and Intermediate Tidal Marsh	2.33	1.08	0.031
Existing vegetation cover (EVC)	0.45	0.23	0.049
Annual precipitation	1.17	0.29	<0.001
$\hat{p}$ intercept	-1.43	0.11	<0.001
Wind speed	-0.26	0.09	0.001
Lunar phase	0.30	0.09	0.003
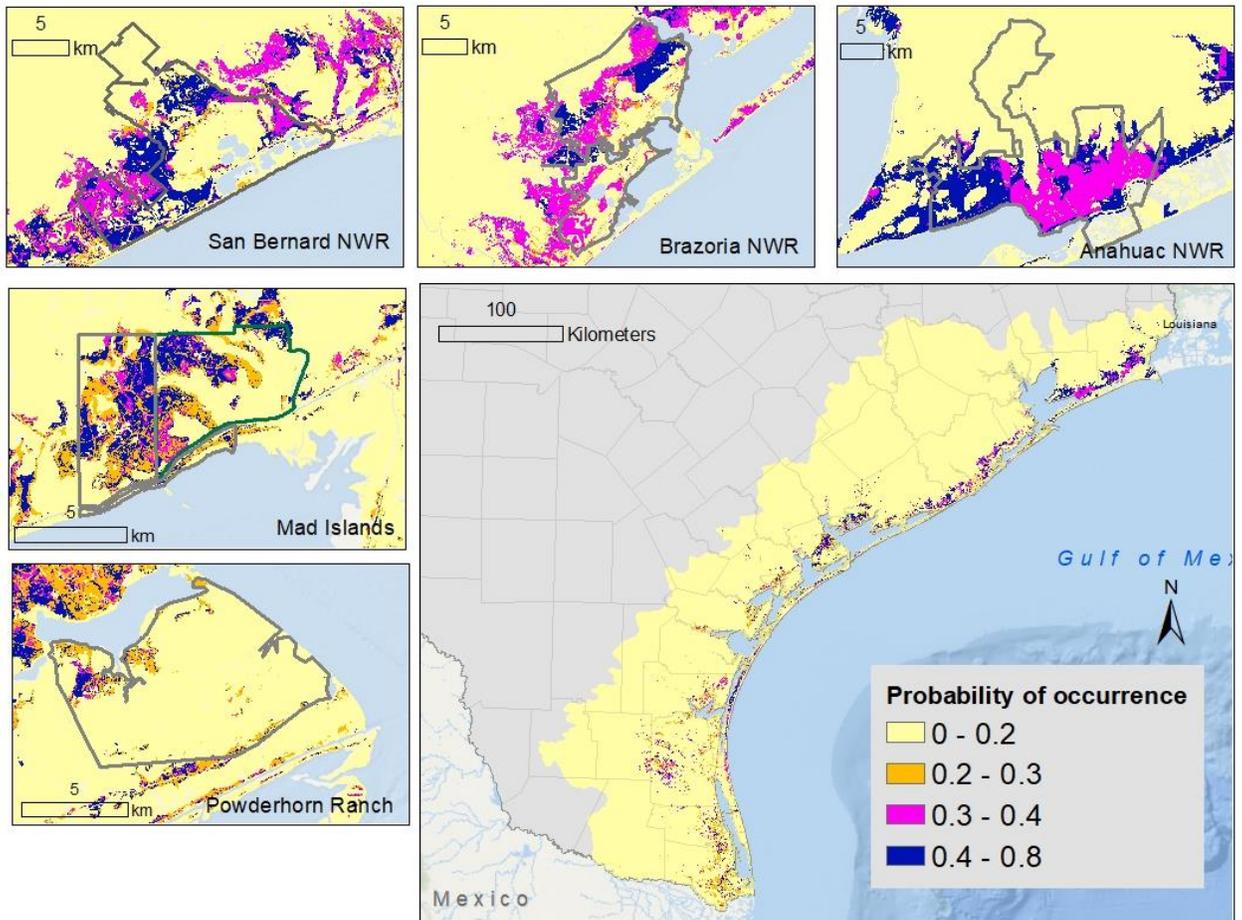
Figure 2-3 Predicted probability of occurrence for the black rail (*Laterallus jamaicensis*) at study sites and along coastal Texas based upon habitat suitability including the variables vegetation type and percent herbaceous cover. Annual precipitation was also influential in the model and positively correlated with black rail occupancy but is not included in this map due to scale differences and insufficient sampling within the range of precipitation values.

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Table 2-6 Predicted probability of occurrence of black rails (*Laterallus jamaicensis*) within coastal Texas study region based upon vegetation type and density of existing vegetation cover.

Probability of occurrence	Number of 30 m² cells	Percent of study region
0-0.2	57013882	94.1
0.2-0.4	362325	0.6
0.4-0.6	2782351	4.6
0.6-0.8	48689	0.1
0.8-1.0	412624	0.7

Table 2-7 Percent of area at study sites in coastal Texas, 2015–2016, that contain habitat with a ≥0.40 predicted probability of black rail (*Laterallus jamaicensis*) occurrence (no predicted probability was >0.70).

Study site	Total pixels	Number of pixels $\hat{\psi} \geq 0.40$	Percent of study site $\hat{\psi} \geq 0.40$
Anahuac NWR	325251	166133	51.1
Brazoria NWR	220883	85564	38.7
San Bernard NWR	165948	58084	35.0
Mad Islands	62753	30632	48.8
Powderhorn Ranch	77152	6694	8.7

Discussion

The secretive tendency of the black rail coupled with the disjunct nature of the species' distribution on a regional and local scale makes it difficult to locate birds. Additionally, the coastal region of Texas spans roughly 695,660 km^2 which makes it difficult to find appropriate areas to survey, especially since the majority of the state is privately owned and access is limited. In this study, I used habitat associations gathered from field data collected at locations where black rails were detected to extrapolate probability of black rail occurrence onto the broader landscape along the Texas coast. I found that black rail occupancy increased in marsh habitats with high levels (>70%) of herbaceous vegetative cover dominated primarily by graminoids and with sparse woody cover, especially in the Salty Prairie vegetation type ($\hat{\psi} \leq 0.87$). Additionally, black rail occurrence was positively correlated with annual precipitation, with the highest occupancy rates occurring in areas with >120 cm of precipitation annually.

There was a positive association between black rail presence and EVC which makes sense since the species is known for its propensity to remain hidden under the cover of dense vegetation. Of the 286 black rails detected during call play-back surveys, only two birds were sighted by a surveyor, the remaining detections were by detecting calls. The Salty Prairie vegetation type is described as having sites that "…may be nearly monotypic stands of *Spartina spartinae* (Gulf cordgrass)" [35]. The Salt and Brackish High Tidal Marsh also had a high occupancy rate ($\hat{\psi} \leq 0.82$). The irregularly flooded marshes in this vegetation type can be dominated by the cordgrasses *S. spartinae* and *S. patens* and include some forbs such as saltwort (*Batis maritima*), glassworts (*Salicornia* spp.), and sea ox-eye daisy.

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Previous studies in Texas have also reported a positive relationship between cordgrass and black rail occupancy[23,30]. Gulf cordgrass is a bunchgrass that creates dense tufts across the landscape. The narrow leaves of neighboring gulf cordgrass plants become intertwined which seems to create a nearly impenetrable overhead cover for the rails while leaving areas of bare ground in between clumps for the birds to travel and forage unseen from above.

Both Salty Prairie and Salt and Brackish Hight Tidal Marsh vegetation types represent what was observed in the field during black rail surveys and reaffirmed by vegetation surveys. Results of vegetation surveys showed most sites with black rail detections had 50-90% *Spartina* cover (*S. patens* and *S. spartinae*). The Fresh and Intermediate Tidal Marsh vegetation type only occurs east of Galveston Bay and covers the majority of the area in which I surveyed and detected black rails. The description for this system may be somewhat inaccurate since it does not mention gulf cordgrass when in fact it was the dominant plant at many sites based upon my surveys.

In the Salty Prairie, the topography is mostly level and some sites may be inundated by storm surges, but there are microtopographic highs in the form of pimple mounds that remain out of the saltwater. The Salt and Brackish High Tidal Marsh is tidally influenced but containing areas of high-marsh that are less frequently inundated, some only influenced by storm tides. Areas of higher topography such as pimple mounds are an important feature in black rail habitat. In California salt marshes, high tides are known to destroy black rail nests [43,44] and also cause the birds to temporarily flee the marshes for higher ground [45,46] leaving them vulnerable to predation [47]. This is likely the case for black rails in Texas coastal marshes as well.

A central challenge in ecology is understanding what limits a species' abundance and distribution. Organisms respond to environmental cues at multiple spatial scales or selection orders so examining ecological phenomena at a single scale may not explain a broader pattern [48-50]. The selection orders are hierarchical ranging from microsite for nesting and foraging, up to the geographic range [51]. For this study, I combined data on two consecutive spatial scales: habitat level (vegetation type and EVC) and regional population level (annual average precipitation). Including multiple scales in a distribution model has been shown to produce models with more predictive power [49] and may be especially useful for species like the black rail that live in fragmented habitat as they do in Texas [52].

Because of its size, coastal Texas has a wide range of climatic conditions and the unique geographic location of the state is also responsible for variability in the climate. Annual precipitation decreases from east to west, as does average annual gross lake evaporation (Texas Water Development Board 2017 State Water Plan). From online databases such as eBird [53], it is apparent that the vast majority of black rail detections in Texas occur in the Northern Humid Gulf Coastal Prairies [54], which represents a subregion within the Gulf Prairies and Marshes as described by Gould, et al. [31]. This region occurs along the Gulf coast from the eastern border of the state to Victoria, Texas, and is characterized as gently sloping prairie with the original vegetation being mostly grasslands, and with an annual precipitation that varies from 147 cm in the northeast portion to 94 cm in the southwest. The black rail detections on eBird [53] occur as a gradient from high to low with the most detections occurring in the eastern portion of the

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region and very few occurring past Port Aransas. Similarly, the number of black rails detected during this study followed the same pattern.

Seemingly appropriate habitat (*i.e.* Salty Prairie and dense herbaceous cover) occurs towards the southern reaches of the coast, but black rails do not appear to be using this region extensively. It is possible that precipitation is one of the limiting factors for the species along the Texas coast. The diet of black rails consists mainly of small (<1 cm) aquatic and terrestrial invertebrates, including snails, amphipods, isopods, spiders, ants, grasshoppers, earwigs and beetles [55]. Hydroperiod influences invertebrate communities in terms of abundance and diversity in wetlands [56-58]. Since black rails are known to use the most shallow areas of the marsh that contain stable water levels [55], perhaps the Salty Prairie and Salt and Brackish High Tidal Marsh vegetation types are drier in the south Texas region and the invertebrate assemblage sustains fewer black rails.

In any habitat modeling procedure, misclassification of suitable and unsuitable habitat is inevitable. Model errors may be a result of problems inherent in the modeling process or from the complexities of a species' ecology [59,60]. The mapped model predictions were consistent with the black rail detection data. I detected the largest number of black rails at Anahuac NWR ($n = 141$, which constitutes 13.5% of the 1,042 surveys conducted at Anahuac) which also had the highest amount of best predicted habitat, and I detected the lowest number of black rails at Powderhorn Ranch ($n = 0$, where 418 surveys were conducted) which had the least amount of best predicted habitat. The predictive ability of the model was somewhat poor (AUC = 0.67), however, visual assessment of the model performance (*i.e.* mapped occupancy estimates at locations were

black rails were detected) revealed 71% of the black rail detections occurred in habitat with an occupancy probability ≥40%. The remaining 29% of detections were estimated to be in habitat with an occupancy probability of <30%. Upon closer inspection of the occupancy map, most of these points were within a few 30 m^2 pixels from suitable habitat, and a small amount were in misclassified areas of the raster, for instance an area with multiple black rail detections at Anahuac NWR was classified as "row crops" in the vegetation type raster, which is inaccurate. Misclassification of areas can lead to inaccurate occupancy predictions and so ground-truthing GIS data is an important step that should be taken when creating SDM with raster data and before implementing rigorous survey efforts.

At the Mad Islands where I detected relatively few black rails ($n = 28$ detections or 3.2% of the 845 surveys conducted at the Mad Islands), the model showed a relatively high proportion of suitable habitat (48.4% of the refuge). This could be due to misclassifications in the habitat rasters, possibly due to management practices that occurred after or during the classification process. For instance, mowing, grazing, or prescribed fire that were applied after raster data collection could result in a mismatch between the EVC raster classification versus at the time of survey.

A limitation of this study was not being able to survey every combination of vegetation type and EVC, resulting in empty pixels in the map *i.e.* areas with no occupancy prediction. A very low proportion of the study region was predicted to have habitat suitable for black rails: only 5.4% of the study area was predicted to have a probability of black rail occurrence greater than 40%. However, 26% of the study area

contained vegetation types I did not survey and hence contain no occupancy prediction. Surveying these additional vegetation types would help to expand knowledge on black rail occupied habitat.

Similarly, because I did not sample the full range of annual precipitation values across the Texas coast, including precipitation in the occupancy map constrained the occupancy predictions to just the area that included the precipitation values in which I did survey. This, coupled with the lower resolution of the precipitation layer, resulted in a very coarse and less comprehensive view of suitable habitat. When viewing the map presented here, one should keep in mind that it does not take differences in precipitation into account so despite the predictions of suitable habitat in the southwestern reaches of the coast, lower precipitation may decrease occupancy probability. Nonetheless, it is quite possible that this region lacks proper survey efforts and populations have gone undiscovered and thus not recorded in eBird.

The predictive performance of the model was 0.67 which is considered to be satisfactory to good in quality. The performance and accuracy of an SDM is in part contingent upon understanding what habitat covariates may be important to the species in question and on the availability of that data in a GIS format. Although I examined 8 different habitat variables, it is likely that I missed additional variables influencing black rail occurrence that would have improved model discriminatory ability. Additionally, some of the categories within the data I used may be more influential than the analysis showed due to insufficient sampling across all categories. For instance, the 348 survey points analyzed in this study fell across 22 different vegetation types, with the majority of

the vegetation types having less than 10 surveys each. Subsequently, I had to group 19 vegetation types together as "other vegetation type". To obtain meaningful estimates of occupancy, there is a boundary or a threshold number of surveys that need to be conducted and a certain number of "present" sites obtained. For this study, birds needed to be detected at roughly 30% of surveys per vegetation type to avoid convergence issues and obtain reliable estimates of occupancy. This is an inherent problem when modeling rare species as the ratio of present to absent sites is usually high. However, habitat modeling is an iterative process [59] and future studies and datasets may improve power to predict black rail presence.

Black rails have a wide distribution in coastal Texas and the few known populations are disjunct. The habitat suitability map provides baseline information about potentially suitable areas and may help guide efforts to find new black rail populations. As with all models that derive predictor variables from GIS data, initial selection of variables that appear to be important to a species is constrained by the availability of the digital data that approximates those variables. There seems to be an association between black rails and habitats that contain high amounts of cordgrass. This association may be related more to vegetation structure than the plant species since black rails were detected in less homogenous areas. It should be noted that areas that do not include cordgrass should not be immediately discounted - surveys in other vegetation types with structural similarities may be occupied by black rails. While the EVC data was seemingly the best available approximation of the structure of the herbaceous habitats, it may have been inadequate especially considering management practices that frequently change the

structure of the marsh *i.e.* burning and cattle grazing. Numerous studies have looked at occupancy rates of rails in relation to fire regime [61-65] and fire is a tool used in habitat management at each refuge in this study where black rails occurred. While burn data is usually available for wildlife refuges, it is not available in a widescale GIS format that would allow interpolation to the greater landscape. There is a trade-off between including more fine-scale data to improve predictive power of a model, and the wider application of the model [59]. Future studies would benefit from the inclusion of applicable fine-scale data when it becomes available in a large-scale GIS format.

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CHAPTER 3

BLACK RAIL HOME RANGE AND HABITAT SELECTION IN LATE WINTER

AND EARLY BREEDING SEASON IN COASTAL TEXAS

Abstract

The use of habitat by the black rail (*Laterallus jamaicensis*) in coastal Texas is poorly studied. My objective was to estimate home range size and habitat selection to provide data for effective management of the species. From January – May of 2017 and 2018, I took locations of 13 radio-transmittered black rails at San Bernard National Wildlife Refuge, Texas. The mean fixed kernel home range for birds with ≥24 relocations was 2.3 ha, with a mean core area of 0.43 ha. Average 95% MCP home range was 0.98 ha with a mean core area of 0.12 ha. During radio tracking, a black rail nest was found on 19 March, the earliest on record for the state. Birds selected the salt and brackish high tidal marsh, salty prairie, and baccharis shrubland, and avoided the salt and brackish low tidal marsh. Home ranges contained a gently sloping elevational gradient suggesting the importance of access to higher ground on-foot. Protection and proliferation of Salty Prairie and Salt and Brackish High Tidal Marsh is recommended for maintaining black rail populations in coastal Texas.

Introduction

Understanding habitat requirements is imperative for managing and protecting habitat for species of conservation need [1]. Species conservation must begin by protecting the appropriate amount and type of habitats required to maintain a viable population. Also useful is understanding species-specific area requirements[1]. For species that are elusive or shy and therefore difficult to detect and observe, telemetry studies are useful to understand a species' habitat requirements. Radio telemetry can help answer questions and strengthen the knowledge base in many research areas such as home range and

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territory size, movement and habitat relationships, survival, dispersal, breeding behavior, and some aspects of demography [2,3].

The black rail (*Laterallus jamaicensis*) is the smallest member of family Rallidae found in North America. There are two subspecies found in North America, the largely resident California black rail (*L. j. coturniculus*) which occurs in disjunct regions of northern California and in the southwest USA, and the partially migratory eastern black rail (*L. j. jamaicensis*), which primarily occurs along the Atlantic and Gulf coasts, with inland populations in Kansas and Colorado. The birds preferred habitat consists of dense herbaceous vegetation in the higher regions of fresh or salt marshes. The species is difficult to detect and study. Coupled with a shy nature and diminutive size, black rails are very reluctant to fly and more inclined to flee on foot when disturbed, usually remaining completely unseen under dense marsh vegetation. Due to their short stature, black rails are usually confined to moist soil marshes or those with the shallowest water [4].

A commonly used definition of home range is "that area traversed by the animal during its normal activities of food gathering, mating and caring for young" [5]. With reports of dramatic population declines in the east and northeast portion of their range [6], it is possible that Texas one of the last strongholds for Eastern black rails and therefore it is critical for managers to understand area requirements and the habitats birds are using in Texas. Several studies have used radio telemetry to estimate home range and core usage area of black rails [7-9] in Florida, Arizona, and California. No studies, however, have estimated home range of Eastern black rails in Texas and thus there is a critical gap in the knowledge base for the species in the state.

Previous studies on estimating home range of black rails has focused on the Atlantic population of the Eastern black rail and the California black rail. In Florida, male home range size was 1.3 ha while females were 0.62 ha during egg laying and incubation [7]. Though not determined with telemetry, estimates of home range size in Maryland were 3-4 ha [10], and in Virginia, home range mapped by tracking vocalizations of one individual over a period of 7 days in June/July was estimated to be 0.47 [11]. Radio-tagged California black rails at Mittry Lake in Arizona where water levels are stable year-round had a home range of 0.50 for males and 0.44 ha for females during the breeding season [12]. In the breeding season, male California black rails in the tidal marshes of San Francisco Bay had a mean home range of 0.59 ha with a mean core area of 0.14 ha and female home ranges were 0.26 ha, with no intersexual differences in core-area size [8].

Animals select resources in a hierarchical order where higher orders are conditional upon lower orders, and thus represent a finer scale[13]. For instance, habitat selection within a home range is one selection order above home range selection since the availability of each habitat is determined by selection of the home range[13]. First-order selection represents the geographic range of a species, second-order represents the home range of an individual or group, and third-order represents habitat selection within the home ranges[13]. As selection becomes more fine-scale, additional selection orders can be added. The purpose of this study was to better understand black rail habitat requirements during winter and early breeding season by examining home range size and habitat selection within each individual's home range (third-order selection) through the use of radio telemetry. I investigated habitat availability and black rail utilization of different

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vegetation types. I also extracted elevation data within home ranges. Since black rails

may select foraging and nesting sites based on water levels [7,9] and can be adversely

affected by fluctuating water levels, elevation is an important aspect of the species'

habitat, especially tidally influenced areas [13-17].

Methods

Study site. I used radio telemetry to examine the home ranges of black rails at San

Bernard National Wildlife Refuge (SBNWR) located in Brazoria and Matagorda

Counties (Figure 3-1). The refuge consists of 11,100 ha of salt marsh habitat

characterized by average precipitation of 145.39 cm, average temperature of 6.5°C in

winter and 33.2°C in summer (Brazoria County, http://brazoriacountytx.gov/). Black rails

were captured on the main refuge property as well as in the Sargent Unit. Locations

containing known populations of black rails were selected for relative ease of access

since tracking required multiple visits at each location per day. Dominant vegetation in

areas where this study was conducted included gulf cordgrass (*Spartina spartinae*),

marshhay cordgrass (*Spartina patens*), sea ox-eye daisy (*Borrichia frutescens*), batis

(*Batis maritima*), and glassworts (*Salicornia* spp.).

Figure 3-1 Location of black rail (*Laterallus jamaicensis*) radio telemetry study areas at San Bernard National Wildlife Refuge, Texas, winter 2017 and 2018.

Capture and radio marking. I captured black rails from January to May of 2017 and 2018 using the bottle-line method or an audio-lure method, both of which were conducted at least 30 min after local sunset. The bottle-line is a 15 m length of rope weighted with five small paint cans spaced ~1.5 m apart along the rope. The cans contain various objects (rocks, jingle bells) that create noise and cause a physical disturbance when dragged through the vegetation. Each crew member had a headlamp and/or hand-held spot-lights to locate flushed birds. Two people held opposite ends of the rope and walked slowly, remaining equidistant to each other while two other crew members walked ~2 m behind the rope. Each person was spaced ~5 m from each other. We used dip-nets to

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capture any black rails that flushed. For the audio-lure method, we would carefully walk through areas occupied by black rails playing black rail calls on portable speakers in attempt to elicit a response. Once a black rail responded, we repeatedly played calls to lure the bird out of the vegetation where we were able to either hand-capture the bird or capture with small (20cm) aquarium fish nets. Black rails were fitted with 0.9g radio transmitters (model BD-2, Holohil Systems Ltd., Carp, Ontario, Canada). Published data on black rail mass in Texas is sparse, however average mass of 10 birds from a previous report was 37.4g[18]. Birds from the east coast, Midwest, and Florida range 26.5 - 44.0 g[4] and the average mass for the California subspecies is 29.3 g [19]. The general rule of thumb is to attach transmitters that do not exceed 3% of the animal's body mass [2]. Birds were weighed upon capture to ensure the transmitters did not exceed 3% of the bird's body mass, meaning birds needed to weigh at least 30g. Transmitters were glued to the bird's back using Loctite® Epoxy Gel with a 6-minute setting time (Henkel Corporation North America). One person would hold the bird and spread the body feathers on the birds' back between the scapulae to reveal bare skin. A second person would roll the transmitter in the epoxy and then place on the skin and then smooth the feathers over the transmitter attempting to attach as many feathers as possible to ensure attachment. After a transmitter was set in place, the bird was held quietly with a hand cupped over their back to prevent wing flapping for five minutes before being placed in an observation pen for another five minutes. Birds were then inspected to ensure that the glue was dry and that the bird's wings were free from the glue. Black rails were captured and marked under a USGS banding permit (#23546), Texas Parks and Wildlife Scientific Collection Permit (SPR-

0106-005) and approved IACUC protocol (IACUC201533955) through Texas State University, San Marcos.

Radio Telemetry. Radio-tagged black rails were located using the homing method or by triangulation [20], with hand-held three-element Yagi antennas and receivers (Model R4000, Advanced Telemetry Systems, Inc., Insanti, MN). When homing, I would approach rails within five meters and record a GPS waypoint to estimate location (Garmin GPS eTrex 20x, WAAS enabled <3 m position accuracy, Garmin International, Inc., Olathe, KS). Upon hearing my approach, or if I made a loud noise such as clapping my hands, birds would often vocalize ("ticky-tick" call) which helped to confirm location. To minimize impact on the sensitive vegetation in the birds' habitat and reduce potential of trampling nests, triangulation was used as the season neared spring when nesting was more likely. Two observers would stand within 20 m of tracked birds and take bearing and waypoints simultaneously at an angle close to 90-degrees between bearings. A third bearing and waypoint were then taken immediately after by one observer quickly walking a few paces to a location in between the first two bearings. Birds were estimated to be at the center of the resulting error triangle.

Birds were tracked from February to May of 2017 and 2018 and relocated 1–4 times daily until the transmitter fell off. Bird locations were obtained ≥1 hr apart to reduce potential autocorrelation among locations [20]. Tracking sessions were conducted daily between 30 min prior to sunrise and 30 min after sunset, and at least once during each hour of the day. Since black rails are reportedly inactive at night [9], I did not regularly track birds after sunset.

Home range. The oldest and most commonly used home range estimation method is the

minimum convex polygon (MCP) [21]. The MCP method measures the area within all, or a

certain percentage of, *i.e.* 95%, relocations. The major disadvantage with this method is

that it can result in overestimation of home range size [20]. I estimated the 95% MCP home

range sizes here for comparison to other studies [7,9]. The second home range estimator I

used, fixed kernel density, accounts for intensity of use of areas within the home range

and excludes areas used minimally [20]. The smoothing parameter specified in conjunction

with the kernel density method controls the "width" of the kernel functions placed over

each relocation. I calculated 95% (home range) and 50% (core use area) fixed kernel

density using likelihood cross-validation (CVh) smoothing parameter. I selected CVh

because it performs well with sample sizes <50 compared to least-squares cross-

validation, another commonly used smoothing parameter [22].

I calculated CVh in Animal Space Use 1.3[23], and the MCPs and kernel density

estimates using the R package "rhr" [24]. To determine the minimum sample size of

relocations required to reliably estimate home range, I created observation-area curves [25]

for a subset of birds monitored >10 days (*n* = 5). For each of these birds, I calculated area

of home ranges with an increasing number of randomly chosen relocation points

beginning with three points and adding one point until all relocation points were drawn [25-

27]. Home range size did not ostensibly increase after 20-25 relocations (see Supplemental

Fig. 3.2). Home range was analyzed for birds with at least 24 relocations (*n* =4), which

was the suitable number of relocations determined by the observation area-curve

analyses. For sake of comparison to other studies, I also analyzed home range for those with at least 10 relocations (*n* = 13).

Habitat selection. To examine habitat selection, I extracted raster data from within home ranges and from the greater study area surrounding home ranges using ArcMap Spatial Analyst [28]. Spatial data included vegetation type from The Ecological Mapping Systems of Texas (EMST) (https://tpwd.texas.gov/gis/programs/landscape-ecology/by-ecoregion-vector/western-gulf-coastal-plain, accessed June 2018) and lidar data for the Texas Mid-coast National Wildlife Refuge Complex (obtained directly from USFWS). The EMST is a land classification map for Texas with a 10 m spatial resolution. The map delineates large-scale ecosystems which are each described by geology, landform, soils, and multiple vegetation types. The vegetation types are described by typical plant assemblages and dominant species. To delineate the greater study area and thus available habitat, I drew polygons in ArcMap that encompassed all home ranges (see Figure 3-1). Ten vegetation types could be found in the study area (Table 3-1). I used the Agresti–Coull-adjusted (ACa) confidence interval method to determine preference or avoidance of vegetation types, where CI < 1 indicates avoidance, CI > 1 indicates preference, and CI overlapping 1 indicates neither *i.e.* use is proportionate to availability [29]. Relocation data was pooled for all birds in the calculation of ACa confidence intervals. The lidar data contained a digital elevation model (DEM, bare ground) from which I extracted elevation data from within the study area and from within home ranges.

Table 3-1 Descriptions (partial) from Elliott [30] of vegetation types found in study area where black rails (*Laterallus jamaicensis*) radio telemetry study took place at San Bernard National Wildlife Refuge in Texas.

Vegetation type	Description
Gulf Coast: Salty Prairie (MoRAP code: 2207)	Saline soils, generally near-coast. Sites may be nearly monotypic stands of *Spartina spartinae* (Gulf cordgrass). Forbs are generally uncommon but may include *Borrichia frutescens* (sea ox-eye daisy). Shrubby species may invade the prairie, commonly including *Iva frutescens* (shrubby sumpweed).
Columbia Bottomlands: Grassland (MoRAP code: 4707)	Herbaceous dominated sites occupying bottomland soils and lacking significant shrub or overstory canopy cover. Mostly managed grasslands dominated by *Cynodon dactylon* (bermudagrass), *Paspalum notatum* (bahiagrass), and *Lolium perenne* (Italian ryegrass).
Columbia Bottomlands: Evergreen Shrubland (MoRAP code: 4705)	Shrublands or sparse woodlands, often the result of disturbance, with well-developed shrub layer with species such as *Ilex vomitoria* (yaupon), *Sabal minor* (dwarf palmetto), *Quercus virginiana* (coastal live oak), *Rosa bracteata* (Macartney rose), or *Baccharis* spp. (baccharis).
Columbia Bottomlands: Herbaceous Wetlands (MoRAP code: 4717)	Wetlands dominated by herbaceous species such as *Carex* spp. (carices), *Eleocharis quadrangulata* (squarestem spikesedge), *Rhynchospora* spp. (beaksedges), *Juncus* spp. (rushes), *Sagittaria* spp. (arrowheads), *Saururus cernuus* (lizard's tail), E*chinodorus cordifolius* (heartleaf burhead), *Typha* spp. (cattails), and/or *Polygonum* spp. (smartweeds).
Coastal: Sea Ox-eye Daisy Flats (MoRAP code: 5605)	*Borrichia frutescens* (sea ox-eye daisy) is the clear aspect dominant of these irregularly flooded sites. These flats become very extensive from Corpus Christi Bay, southward.
Coastal: Salt and Brackish Low Tidal Marsh (MoRAP code: 5607)	Marshes frequently inundated by tides and often dominated by *Spartina alterniflora* (smooth cordgrass).
Coastal: Salt and Brackish High Tidal Marsh (MoRAP code: 5617)	Irregularly flooded marsh dominated by graminoids such as *Spartina patens* (marshhay cordgrass), *Distichlis spicata* (saltgrass), and *Schoenoplectus* spp. (bulrushes).
Native Invasive: Common Reed (MoRAP code: 9107)	Areas mapped within this type are often dominated by nearly pure stands of *Phragmites australis* (common reed) on formerly disturbed soils.
Native Invasive: Baccharis Shrubland (MoRAP code: 9116)	Salty or sandy soils and *Baccharis* spp. (baccharis), *Prosopis glandulosa* (honey mesquite), *Tamarix* spp. (salt cedars), and *Iva frutescens* (shrubby sumpweed) are the most common dominants.
Non-native Invasive: Chinese Tallow Forest, Woodland, and Shrubland (MoRAP code: 9204)	More or less dense stands of *Triadica sebifera* (Chinese tallow) characterize this type, which is generally mapped over prairie soils, but a diversity of mainly invasive deciduous shrublands and sparse woodlands are circumscribed.

Results

Home range. A total of 16 birds were captured and tracked: 9 from February – May

2017, and 7 from February – April 2018. Average bird mass was 38.5g (SD = 5.2) and no

bird weighed less than 30.0g. I obtained an average of 22 (SD = 9.7) relocations per bird

and transmitters stayed attached from 3 to 34 days ($\bar{x} = 10.6$). Twelve of the deployed

transmitters were relocated after birds pulled them off. The other two were on birds that

left the area and could not be located. The 95% MCP home ranges for the birds with ≥24

relocations averaged 0.98 ha (SD = 0.26), and for the birds with ≥10 relocations: 0.52 ha

(SD = 0.36, Table 3-2). For the birds with ≥24 relocations ($n = 4$), which consisted of all

males, the kernel home range averaged 2.3 ha (SD = 0.97), and core use area averaged

0.43 ha (±0.17 SD). There was another bird with >24 relocations that was excluded from

all reported estimates since the bird's home range was exceedingly larger than the others

(kernel: 23.2 ha, MCP: 6.1 ha). For the birds with ≥10 relocations, which consisted of

nine males and four females, kernel home range averaged 1.6 ha (SD = 0.95), and core

use area averaged 0.35 ha (SD = 0.16). The kernel home range did not differ (*t*-test: $P >$

0.05) between years or between males ($n = 9$, $\bar{x} = 1.83$ ha, SD = 1.0) and females ($n = 4$,

$\bar{x} = 1.49$ ha, SD = 0.97) and MCP home ranges of birds did not overlap except for those

of two male and female pairs captured together. A black rail nest was found on 19 March,

the earliest on record for the state and is described in detail in the Supplementary

Materials section.

Table 3-2 Means (±SD) of home range (95%) and core use area (50%) of radio-marked black rails (*Laterallus jamaicensis*) captured at San Bernard National Wildlife Refuge, Texas, winter and spring 2017 and 2018.

Home range estimation method	≥24 relocations (*n* = 4)	Range	≥10 relocations (*n* = 13)	Range
Fixed kernel density				
Home range (ha)	2.30 (±0.97)	1.23 - 3.53	1.57 (±0.95)	0.46 - 3.53
Core area (ha)	0.43 (±0.17)	0.28 - 0.65	0.35 (±0.16)	0.13 - 0.65
Minimum convex polygon				
Home range (ha)	0.98 (±0.26)	0.61 - 1.22	0.52 (±0.36)	0.11 - 1.22
Core area (ha)	0.12 (±0.05)	0.08 - 0.18	0.10 (±0.5)	0.02 - 0.18

Habitat selection. The largest proportion of the vegetation in the study area was Salt and Brackish Low Tidal Marsh (77.8%), followed by Salty Prairie (9.8%), Salt and Brackish High Tidal Marsh (9.2%), and Baccharis Shrubland (1.5%, Table 3-3). The other six vegetation types (listed in Table 3-1) combined made up the remaining 1.3% of the study area. The most common vegetation type found within black rail home ranges was Salty Prairie (51.4%), followed by Salt and Brackish Low Tidal Marsh (20.4%), Salt and Brackish High Tidal Marsh (17.7%), and Baccharis Shrubland (10.3%). No other vegetation types fell within home ranges. Black rails did not use vegetation types in proportion to their availability: the rails preferred Salty Prairie (95% CI [2.9, 3.3]), Salt and Brackish High Tidal Marsh (3.3, 3.6), and Baccharis Shrubland (12.5, 13.0), and avoided the Salt and Brackish Low Tidal Marsh (0.04, 0.49). Zonal statistics within each home range indicated mean elevation was 67.0 cm, range: 26.4 – 145.3 cm. The average

elevation gradient within home ranges was 52.3 cm. Mean elevation within the study area

was 82.9 cm, range: -13.4 – 248.0 cm.

Table 3-3 Vegetation types significantly ($\alpha = 0.05$) selected against (-) or selected for (+) within home ranges of 13 radio-marked black rails (*Laterallus jamaicensis*) captured at San Bernard National Wildlife Refuge, Texas, winter and spring 2017 and 2018.

Vegetation type	Number of relocations	Percent of all home ranges	Percent of available area
Gulf Coast: Salty Prairie (+)	85	51.4	9.8
Coastal: Salt and Brackish Low Tidal Marsh (-)	56	20.4	77.8
Coastal: Salt and Brackish High Tidal Marsh (+)	90	17.7	9.2
Native Invasive: Baccharis Shrubland (+)	53	10.3	1.5

Discussion

At SBNWR in Texas, male black rails had home ranges that were somewhat smaller in size (MCP range: 0.61 - 1.22, $\bar{x}$ = 0.98 ha) than those estimated in Florida (MCP range: 0.51 - 3.1 ha, $\bar{x}$ = 1.3 ha [7]). Florida estimates were measured during egg-laying and incubation and estimates in Texas were obtained during winter and into breeding, with most birds tracked during winter. Studies of other members of Rallidae have found seasonal variation in home range size [31,32], however non-breeding home ranges were larger than breeding home ranges. Smaller home ranges in coastal Texas might indicate resource stability within home ranges during winter. Other reasons home ranges may be smaller in Texas than in Florida include regional habitat differences or density-dependent factors such as population size [33] and intraspecific competition [34]. Since this study was conducted primarily during winter, seasonal variation in home range

size is unknown. At Mittry Lake WMA in Arizona, home ranges of California black rails did not vary seasonally [12], the authors suggesting this may be due to the study area having relatively stable water levels throughout breeding and winter. At San Bernard NWR, droughts, floods, freezes, and fire likely cause resources to fluctuate so black rail home ranges may indeed change seasonally and further research is warranted.

The nature of black rail territoriality is poorly known and has been described as confusing [4]. I captured multiple neighboring birds and tracked them simultaneously. Besides male and female black rails captured together, MCP territories did not overlap indicating birds are potentially territorial over the winter. The outlier bird with the comparatively large home range was a male and most likely a second-year bird, according to plumage characteristics outlined by Pyle [35]. This bird made more large-scale movements than any other tracked bird and did not appear to have a core use area, coinciding with "wandering activity" seen in winter and post-nesting in Arizona [12], and mentioned by Todd [36]. This bird made one exceptionally large movement during one tracking session of roughly 415 m within 2 hours. Overall, I tracked this bird for 11 days in early March before he ostensibly left the area and was not relocated again.

The Salty Prairie was the most common vegetation type within home ranges (>50%). The Salty Prairie is described in part as having sites dominated by gulf cordgrass "…sometimes to the near exclusion of other species" [30]. Forbs found in this vegetation type include *B. frutescens, Solidago sempervirens* (seaside goldenrod), and *Iva angustifolia* (narrowleaf sumpweed). During radio tracking, gulf cordgrass was observed as the dominant species in all but one of the home ranges. Similarly, Tolliver, et al. [37] reported

that black rail abundance and occupancy increased with cordgrass at sites along the Texas coast. The clumpy and dense nature of this grass provides visually impenetrable cover for black rails as well as refuge from high water levels since the birds can climb into the matrix created by the leaf blades. Since black rails were selecting Salty Prairie disproportionately higher that its availability in the greater landscape, management focuses should be on the protection and proliferation of this vegetation type.

Roughly 40% of the remaining vegetation types within home ranges was split almost evenly between the Salt and Brackish High Tidal Marsh and the Salt and Brackish Low Tidal Marsh. These marshes are found in relatively low-lying areas where some sites have regular tidal influence and others may be influenced only by storm tides [30]. The composition of these vegetation types is primarily related to tidal hydroperiod. The areas with decreased frequency of tidal inundation are known as the high marsh and may be dominated by marshhay cordgrass, gulf cordgrass, bullrushes (*Schoenoplectus* spp.), saltgrass, and forbs such as glassworts and sea ox-eye daisy [38]. The shrubby forb sea ox-eye daisy was commonly observed to varying degrees within all home ranges. This plant species occurs in areas with higher salinity and slightly lower elevations that gulf cordgrass and could indicate areas of wetland depression that retain water longer than the surrounding *Spartina* marsh. The lower marsh is described as being frequently inundated by tides and often dominated by smooth cordgrass (*Spartina alterniflora*) [30]. California black rails in Arizona were found to use the dryer areas of the marsh, closer to upland vegetation [9]. Similarly, black rails at SBNWR selected the Salt and Brackish High Tidal Marsh at a greater proportion than its availability, whereas the Salt and Brackish Low

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Tidal Marsh was used proportionally less than its availability. This may indicate these lower areas are avoided, especially if water levels are too high. Black rails may be similar to Yellow Rails (*Coturnicops noveboracensis*) who have been labeled the "Goldilocks of Rallidae" for their preference for water that is not too deep and not too shallow [39]. Home ranges contained about 10% Baccharis Shrubland which describes areas that have been invaded by woody species such as baccharis (*Baccharis* spp.), shrubby sumpweed (*Iva frutescens),* honey mesquite (*Prosopis glandulosa*), and salt cedars (*Tamarix* spp.). The precise density of woody vegetation in this azonal type may vary since woody encroachment levels in marshes at SBNWR fluctuate regularly due to controlled burning implemented to limit invasion of woody plants [40]. There were scattered baccharis shrubs in most home ranges and areas of dense baccharis bordering some home ranges, but no tracked birds were ever located within overtly woody areas. However, since large areas of woody shrubs are not conducive to using the bottle-line method of capturing birds, it was not possible to target these areas for birds. Future studies are necessary to determine if woody areas are used by black rails. The elevation within home ranges varied by roughly one-half meter. An elevational gradient is not readily apparent on the landscape and thus represents a gentle slope. An elevational gradient may be an important feature that would allow the birds to easily use their preferred travel method of walking to higher ground during periods of flooding. Elevation has been found to influence nest-site selection in other marsh birds including clapper rails (*Rallus crepitans*) and saltmarsh sparrows (*Ammospiza caudacutus*), which typically build nests in areas higher than the surrounding habitat [41,42]. Furthermore, there are numerous accounts of black rail nest

failure due to flooding [15,17,43], not only from tidal influx but from heavy rain as well [7]. Black rails are known to nest on the ground[43], just a few cm off the ground [44-46], and to up to 30 cm off the ground[15]. Nest height is probably influenced by area-specific hydrology and predation factors.

The sample size for this study was small and the proportion of birds with ≥24 relocations was even less ($n = 4$). The black rail nest was found in late March which was earlier than I had anticipated for the species to be nesting. To avoid trampling nests, I subsequently ended bottle-line capture a month earlier than planned in the second season which probably reduced sample size of radio tagged birds. Ideally, one would obtain a suitable, equal number of locations for each individual, but there are many uncontrollable factors that can get in the way. For instance, the transmitter can fall off or be pulled off by the animal, the battery can fail, or the animal can disperse. The number of geographic locations required for a robust estimate of home range has long been an important question in spatial ecology [25,27,47]. As the number of locations increases, so does the home range size until an asymptote is reached from sampling saturation [2]. The observation-area curves I calculated indicated that home ranges did not increase after 20-25 locations. Similarly, home range size of King Rails in coastal Texas and Louisiana did not increase after 20-25 locations [48], but for California black rails in the San Francisco Bay area, 10 relocations were found to be enough to create an asymptote [8]. Other black rail telemetry studies did not take number of relocations per bird into consideration when calculating home ranges.

The sample of four birds with ≥24 relocations consisted of all males which may have caused the estimate to be biased since male black rails in Florida were found to use larger home ranges than females [7]. To include data from as many of the radio-tracked birds as possible, I also calculated average home range size for birds with a relatively low number of relocations *i.e.* ≥10. Including these birds in the sample caused a 0.7 ha decrease in average kernel density home range. This could have been due to the inclusion of females that may have a smaller home range, or from inadequate numbers of relocations for the other birds. I tracked over twice as many males as females and my findings of no significant difference between sexes may be due to high variances and low samples sizes, which reduces power of tests.

Part of the problem in obtaining a large sample size was the difficulty of capturing black rails. The bottle-line method worked reasonably well and is how I captured most of the birds in this study. The call-playback lure method that was employed after the possibility of nesting began was highly unreliable. I also tried a mist-net method used by Hall and Beissinger [49] with California black rails but results were poor. Numerous studies have used drift fence and door-drop traps [7,9,46,50] with great success, possibly due to relative ease of blocking off travel lanes via drift fences in certain habitat situation, for instance areas restricted by a road or shoreline [12]. It may be warranted to incorporate traps in capture methodology for future studies in Texas, however difficulty in blocking travel lanes in the large expanses of habitat may prove to be a challenge. Incorporating call play-back at traps may improve capture chances. Perhaps the most important

consideration with using a box trap in Texas is the high levels of red imported fire ants (*Solenopsis invicta*) in some areas, which could cause direct mortality of trapped birds.

The other difficulty in obtaining a suitably large sample size was getting transmitters to stay affixed long enough to obtain an adequate number of relocations. Transmitter attachment is a serious consideration since improperly attached transmitters may alter the bird's behavior or cause death. There are various transmitter attachment methods used on birds including wing loop harnesses, tail clips, subcutaneous sutures, and numerous types of adhesives [51,52]. During a pilot study, I used cyanoacrylate (aka: "super glue") which only held transmitters in place for about one day. I considered using a harness with a waist loop but was concerned with permanence of the harness on the bird. Since epoxy was working well enough, I abandoned the idea of using harnesses. When using epoxy for transmitter attachment, I found optimal placement to be high on the birds back to make it more difficult for the bird to reach and pull off.

Black rails at SBNWR selected home ranges in habitats with little to no tidal influence and were dominated by dense graminoids, especially cordgrasses (*S. spartinae* and *S. patens*). As water levels fluctuate and seasonal drying occurs, the rails probably use lower areas that retain water, so these areas are likely still important. Home ranges may shift in size and location according to hydrologic conditions, as well as other factors related to vegetative cover. Future studies focusing on understanding seasonal movements of black rails would help to better inform conservation and management efforts in coastal Texas.

Supplementary Material

Black rail nest. During radio tracking on 19 March 2018, I incidentally located one black rail nest that contained a single egg. I presumed this nest belonged to one of the radio-tagged birds since the dropped transmitter (the bird had apparently pulled it off) was located directly under the nest. The nest was constructed in a clump of *S. spartinae* and appeared to be made entirely of *S. spartinae* and a few black rail feathers. The rim of the nest was ~16 cm from the ground and the nest bowl measured 8.0 cm in diameter and 1.5 cm deep. The surrounding vegetation consisted of ~75% *S. spartinae* and *B. fructescens*, ~20% *Monanthochloe littoralis* (key grass), with small amounts of *Distichlis spicata* (saltgrass), *Lycium carolinianum* (Carolina wolfberry), *Salicornia* spp. and *Cuscuta* sp.(dodder). The surrounding canopy height of the vegetation was ~70 cm. I did not approach the nest for three days after it was initially located but when I eventually returned to the nest it appeared unchanged and ultimately the birds abandoned the nest and the egg.

Known nesting dates for Eastern black rails include 30 April through 15 August [4]. There is very little data on black rail nesting in Texas: Oberholser [53] indicates nesting dates of 9 May in Galveston and 5 June at Brazoria NWR. The knowledge of this early nesting date is an important finding for Texas since many marshes are managed in part with controlled burning. Compared to mean nest height for nests in Florida, the rim of the nest I found was over twice as high. As previously mentioned, black rails show great variation in nest height, even within the same marsh [43].
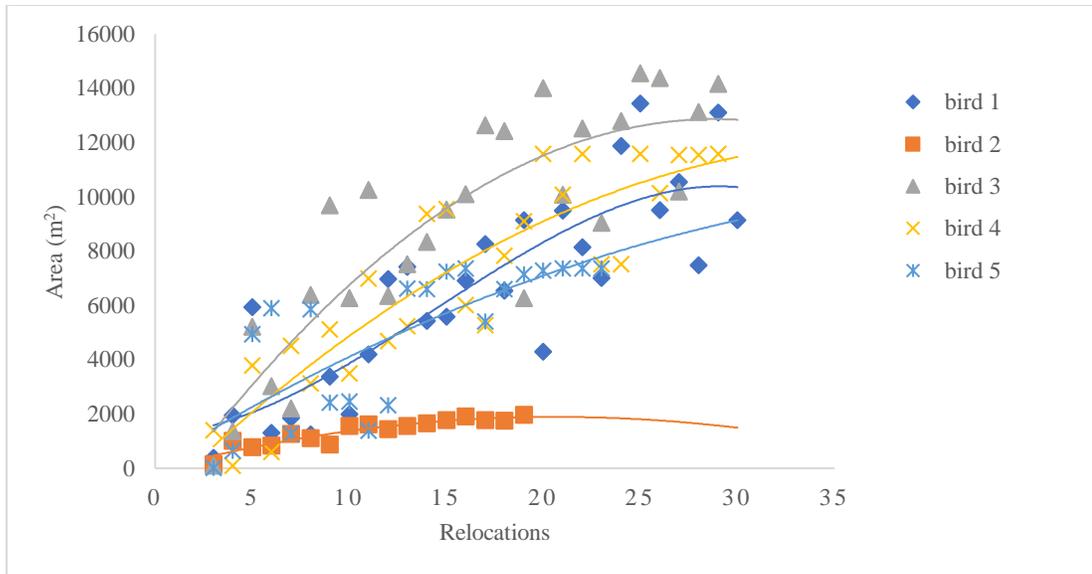
Supplemental Figure 3-2 Observation-area curves for five black rails radio-tracked for >10 days at San Bernard National Wildlife Refuge, Texas in 2017 and 2018.

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CHAPTER 4

WINTER INTERSPECIFIC DENSITY RELATIONSHIPS BETWEEN BLACK RAILS

AND YELLOW RAILS IN THE CONTEXT OF FIRE IN COASTAL TEXAS

Abstract

Prescribed fire is widely used as a management tool in Texas coastal ecosystems. During winter, coastal marshes at San Bernard National Wildlife Refuge in Texas provide habitat for both resident and migratory black rails (*Laterallus jamaicensis*) and migratory yellow rails (*Coturnicops novaboracensis*). The populations of these species are believed to be influenced by fire regime, but information is lacking for these species in Texas. In 2017 and 2018, systematic bottle-line surveys targeting black rails and yellow rails were conducted in six plots at SBNWR that differed in months post-burn ranging from 3 to >86. Effects of months post-burn and habitat variables on the density of each species were assessed using generalized linear mixed models. I also used linear mixed effects models to compare habitat variables measured where birds were flushed to examine how fire history affected habitat variables among plots. Over two winters, for all plots combined I captured 75 rails: 12 black rails and 63 yellow rails. Rails were captured in each of the six plots during the first year. Two plots were burned in a wildfire in between study seasons and subsequently no rails were detected in those plots. There was no correlation between months post-burn and density of either rail species. Plots varied most in woody frequency and herbaceous vegetation density. There was a positive correlation between woody frequency and months post-burn, however there was no correlation between herbaceous vegetation density and months post-burn. The differences in growth rates of herbaceous vegetation among plots signifies the complex dynamic between fire regime and herbaceous growth. None of the measured habitat covariates were able to explain density of black rails within burn-plots. Black rail density in burn-plots may have been affected by variables not directly measured in this study like food availability, low detectability, or territoriality. Yellow rails tolerated a relatively wide range of burn regimes. Yellow rail density was best explained by herbaceous vegetation density where lower density of vegetation in plots provided conditions attractive to yellow rails. Results indicate burn regime did not act independently to influence habitat dynamics. On San Bernard National Wildlife Refuge, habitat characteristics are more indicative of rail density rather than simply the number of months post-burn.

Introduction

Fire is an essential part of Gulf coast marsh ecology [1], and many coastal marshes are managed through a combination of fall or winter burning, herbicide application, and structural marsh management (i.e. levees and water control structures). Primarily due to human influence, it is likely that natural fire occurs less in coastal marshes than it did historically. Examples of human influence include fire suppression practices, reduction of natural fire starts due to conversion of land for agriculture, as well as the construction of ditches, roads and levees that can serve as firebreaks and affect fire spread. In the Texas Gulf Coast region, the reduction of fire disturbance has allowed encroachment of some woody species like eastern baccharis (*Baccharis halimifolia*) and also cordgrasses *(Spartina patens* and *S. spartinae)* to form dense, homogenous stands, which are less diverse than marshes in which burning creates a mosaic of plant communities [2].

When the U.S. Fish and Wildlife Service (USFWS) first recognized controlled burning as an important marsh management tool over 70 years ago, it was initially concerned with waterfowl management on Gulf coast refuges. Prescribed fire was often used to remove plants of little or no use to hunted species and stimulation of food plants eaten by waterfowl [1]. Nonetheless, the purposes of burning vary depending on management goals. Burning can help limit the encroachment of woody vegetation or dominant plant species, remove the litter layer, and improve and maintain the marsh habitat for waterfowl, muskrats (*Ondatra zibethicus*) and American alligators (*Alligator mississippiensis*) [1,3-5]. The USFWS current use of frequent fires in management practices in the Texas Mid-Coast National Wildlife Refuge Complex (TMC) is aimed at

maintaining or recovering a grass-dominated ecosystem in former marshland and prairies [6].

Avian guilds such as grassland birds, rails, and waterbirds that inhabit fire-dependent ecosystems are directly influenced by spatial and temporal heterogeneity created by fire [3,7-9]. Prescribed burning in coastal marshes can also have indirect effects on non-target species by altering vegetation structure, the amount and distribution of open water, and the quality and availability of food items [4,5,10,11]. Understanding avian responses to management practices such as controlled burning is essential to maximize conservation efforts.

The eastern black rail (*Laterallus jamaicensis jamaicensis*) is a marsh-dependent bird that inhabits some inland freshwater wetlands and coastal "high" marshes (characterized by infrequent tidal inundation) in the eastern United States. It is the smallest rail in North America and has a broad, patchy distribution. Black rails are a secretive species and are reluctant to fly, preferring to keep hidden under the cover of dense herbaceous vegetation, and moving about primarily on the ground. Preferred habitat for the species includes moist areas dominated by fine-stemmed plants such as cordgrasses, rushes, and sedges [12].

The yellow rail (*Coturnicops noveboracensis*) is the second smallest rail in North America and is known to be almost as secretive as the black rail [13]. Like black rails, yellow rails are difficult to survey and reluctant to fly. The species is listed as endangered or threatened in some states, a Species of Conservation Concern in Canada [14], and as a

Migratory Nongame Bird of Special Management Concern by the U.S. Fish and Wildlife Service [13,15]. Yellow rails breed in northern United States east of the Rocky Mountains, and the eastern two-thirds of Canada to the Atlantic coast. The species over-winters along the Atlantic coast from North Carolina south to the Florida coast, along the Gulf coast to the Texas mid-coast, and yellow rails were recently discovered overwintering in Oklahoma [16].

In Texas, black rail and yellow rail wintering ranges overlap. Butler, et al. [17] estimated the yellow rail population overwintering in one sampled marsh at San Bernard NWR (SBNWR) in Brazoria County, Texas, consisted of $1,170 \pm 300$ individuals, or $\sim 5.2 \pm 1.3$ rails per hectare. Tolliver, et al. [18] estimated mean abundance of black rails during the spring in sites along the Texas coast as $0.02 - 0.08$ rails per hectare. This number might be higher in the winter because preliminary isotope work suggests that the Texas coast harbors migratory, overwintering black rails (J. Wilson, personal communication). Like black rails, yellow rails are generally found in the drier areas of cordgrass marshes and both species appear to consume some of the same food items[12,13]. During winter bottle-line surveys at SBNWR, the two species are often found in the same marshes (J. Wilson, personal communication). Since yellow rails and black rails ostensibly display ecological similarities, it is possible that interspecific (or between-species) competition occurs between the species. Ecological theory predicts that two or more species rarely coexist in the same niche but instead one species will displace the other [19,20]. The intensity of interspecific competition depends upon the similarity of the species use of resources. Nonetheless, closely related species that live in the same habitat

have been found to use the environment in different ways, also known as niche partitioning or niche differentiation [19,21].

Many studies have looked at effects of prescribed fire on species of rails [8,9,22-26]. A study at the Texas Mid-Coast National Wildlife Refuge Complex reported indirect mortality of yellow and Virginia rails (*Rallus limicola*) due to predation by raptors when rails fled from fires[6]. However, in Florida researchers observed direct mortality of black rails from fire during a controlled burn conducted during winter [27]. In marshes within the lower Colorado River floodplain in California and Arizona, the numbers of California black rails (*L. j. coturniculus*) detected within burned plots, both pre- and post-burn, were no different than in unburned plots [25]. A study conducted on an inland eastern black rail population located in Kansas found that black rail detections were high in areas with a moderate level of fire and grazing disturbance but had no detections in areas where haying, burning, and grazing occurred simultaneously [28]. Fire can create a patchy vegetation matrix in wetlands, reducing many areas to bare ground. As black rails are found in habitats that have already been fragmented and much reduced due to habitat loss, increasing our understanding of how fire affects black rails should be a management priority.

Periodic disturbance, such as grazing or fire, might be needed to maintain habitat for yellow rails. Invasion of woody species can diminish the quality of yellow rail breeding habitat [13] and the species' presence on breeding grounds in Michigan was inversely related to time since fire [8,23]. Similarly, two studies found the probability of yellow rails declined with time post-burn in pine savanna wintering habitat along the

Gulf Coast [9,22]. Control of woody encroachment may benefit yellow rails and black rails since it removes perching sites for avian predators. Nonetheless, the relationship between these rails and the prevalence of woody vegetation is unclear. California black rails were discovered in the mid 1990's breeding in marsh vegetation along a creek in an oak ecosystem in California [29] suggesting a high tolerance for woody cover. Similarly, woody cover was not found to influence winter occupancy of yellow rails in pine savanna habitat in Alabama and Mississippi [22].

The objective of this study was to obtain and compare density of wintering black rails and yellow rails in study plots differing in time since burned. The goal was to examine interspecific density relationships, how burn regime affected habitat variables, and which burn regimes contain the highest/lowest numbers of rails. I predicted the responses of yellow rails and black rails to wintering habitat burning would be similar to one another.

Methods

Study area. The study plots were located at San Bernard National Wildlife Refuge (SBNWR), in Brazoria and Matagorda counties, Texas (Figure 4-1). The refuge contains numerous units with salty prairie marsh dominated by Gulf cordgrass, saltmeadow cordgrass, sea oxeye daisy (*Borrichia frutescens*), and eastern baccharis. Fall and winter prescribed burns take place as needed on a 3 to 6-year rotation to maintain an early-successional stage. I selected six ~10 ha study plots that varied in months post-burn (MPB). Plots included the following: 11MPB, 15MPB, 27MPB, 38MPB, 76MPB and

>84MPB. Since the same plots were used during the second year, each plot increased by 12 MPB in 2018, besides two plots that were burned in a wildfire in between seasons. Hereafter, the naming convention of plots will be initials of the unit where the plot was located followed by MPB, e.g. CF-11 represents the plot in the Crawfish unit that was 11MPB.
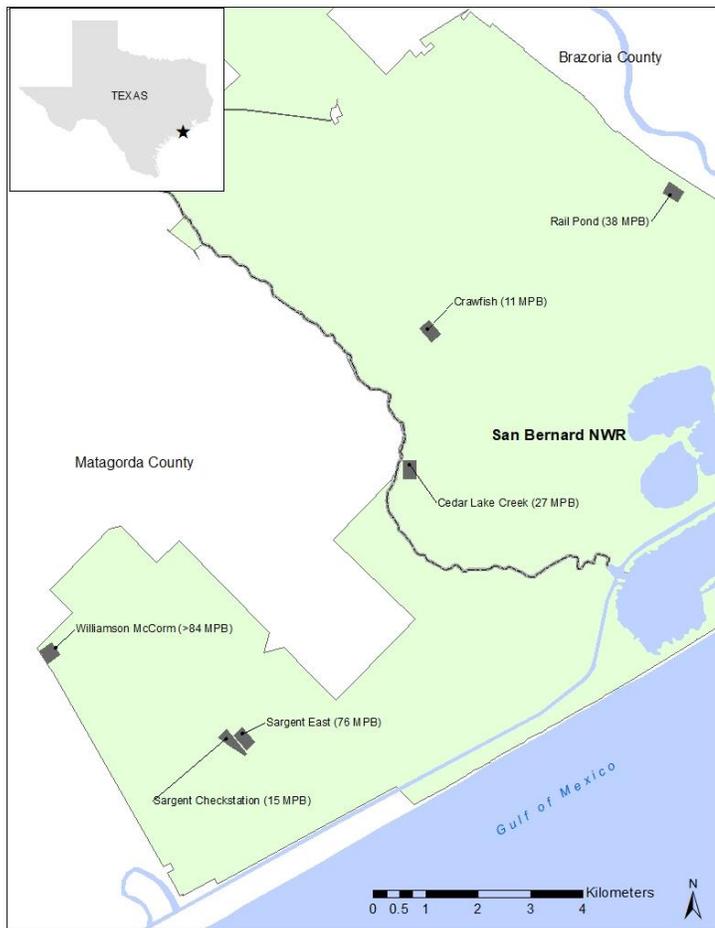
Figure 4-1 Study plots where back rails (*Laterallus jamaicensis*) and yellow rails (*Coturnicops noveboracensis*) were captured and banded during the winter season of 2017 and 2018 on San Bernard National Wildlife Refuge, Texas. Plots differ in months post-burn (MPB). For the 2018 season, MPB increased by 12 for all plots besides Sargent East and Williamson McCormick which were burned in a wildfire three months prior to the field season.

Survey methods. Since rails are characteristically secretive, most population techniques rely on vocalizations to detect and count rails. Nonetheless, population techniques that detect vocalizations are unpractical in winter because rails rarely vocalize at this time of year. Instead, the bottle-line method was used to capture and band black rails and yellow rails from January through March 2017-2018. I conducted surveys with a four-person crew. Bottle-lining began ~30 mins after sunset and ended once the entire plot had been systematically covered by walking along parallel transects or until 2.5 hrs had passed. The bottle-line was a 15m long rope weighted with five small paint cans spaced ~1.5 m apart along the rope. The cans contain various objects (rocks, jingle bells) that create noise and cause a physical disturbance when dragged through the vegetation. Each member of the crew was equipped with a headlamp and/or hand-held spot-light. Each plot was marked at corners and midpoints between corners with PVC pipes that had reflectors affixed to the top. Two people held opposite ends of the bottle line and walked across the plot towards a PVC pipe while attempting to remain equidistant to each other. The other two crew members walked ~2 m behind the rope and each person was spaced ~5 m from each other. I attempted to bottle-line each plot four times each year, prior to April when nesting became more likely, with repeat surveys at the same site roughly three weeks apart. Flushed rails were captured with dip-nets. I affixed a USGS aluminum band and took a waypoint for each bird at the point from where it flushed to conduct a habitat and vegetation assessment at each point the next day. I did not bottle-line when it was raining or when winds were above 16 km per hour. During rains and strong winds the vegetation moved and greatly impaired my ability to detect moving birds.   Habitat

variables were measured in the 50 x 50 m area surrounding each location where a black

rail or yellow rail was flushed. Dominant cover types *i.e.* those that composed >50% of

the vegetation, were recorded for the entire plot. More in-depth measurements were taken

within six randomly selected 10 x 10 m subplots. These measurements included Robel

pole [30] readings, woody frequency measured as tallies of trees species >1 m in height, and

herbaceous overhead cover class for a 1 x 1 m square chosen at random. Robel poles are

used as a visual obstruction measurement to evaluate the height and density of vegetation.

Cover classes were as follows: 0 = bare, 1 = 1%, 3 = 1-5%, 4 = 10-20%, 5= 25-35%, 6 =

40-50%, 7 = 55-65%, 8 = 70-80%, 9 = 85-95%, 10 = >95% cover. I also conducted a

count active mounds of the invasive red imported fire ant (RIFA, *Solenopsis invicta*)

within the 10 m plot. This ant may directly affect a species of bird by eating eggs and

killing chicks [31,32], or indirectly by lowering populations of invertebrate species that

might have been consumed by rails [33,34]. Since the habitat within each plot was typically

uniform due to relatively flat topography of the wetlands, separate measurements for

birds captured within 25 m of one another were not taken unless an obvious difference in

habitat structure was observed *i.e.* a stand of baccharis or a salt pan.

Statistical analysis. To compare differences in habitat features among and between plots

as a response to MPB, I used linear mixed effects models (LMEs) to examine whether the

fixed factor MBP was linearly related to habitat variables (response variables). Burn-plot

was the random factor and the model had an intercepts random effect. I examined

correlations between habitat features for multicollinearity. As overhead cover was

correlated with Robel ($r = 0.41$), I selected Robel to remain in the analyses as an

assessment of density of herbaceous vegetation within plots since it provided a more comprehensive measurement of the vegetation (height and density). The other habitat features included in LME models were woody frequency, and RIFA mound density. I examined whether variation of habitat variables in response to MPB was greater among or within plots using the intraclass correlation coefficient (ICC) [35]. An ICC >0.50 indicates variation in the response variable is higher among plots, while an ICC of <0.05 indicates the variability is greater within plots. The ICC might be useful to know regarding how MPB affects habitat. For example, if a relationship is detected between a response variable and MPB, an ICC >0.50 would indicate that the how burns affect habitat differs from one plot to the next.

To examine black rail and yellow rail densities as a response to differences between burn-plot habitat features, I used generalized linear mixed effects models (GLMMs) where all habitat features were fixed and burn-plot was the random factor. Again, this model had an intercepts random effect. I used a Poisson distribution as the log-link function for GLMM models. Habitat features included in GLMM models were Robel, woody frequency, RIFA mound density, and MPB. I built 16 models: 8 for each rail species. I modeled each habitat covariate alone and then created models with all possible combination of two or three covariates, plus global and null models. Model assumptions for GLMM include normally distributed random effects, use of a link function that is appropriate for the data, and that the estimation of variance is appropriate i.e. no over- or underdispersion. All LME and GLMM models were fit using the package "lme4" in the program R [36]. I used Akaike's information criterion adjusted for small

sample size (AIC$_C$) for model selection. Models with ΔAIC$_c$ values ≤ 2 were considered to have strong support [37]. During the second year, there were three plots where no rail captures occurred; thus, these plots were not included in analyses since habitat variables within these plots were not associated with the occurrence of either rail.

Results

Bird captures. Between 23 January and 27 March 2017, and 24 January and 19 March 2018, I conducted 84 bottle-line surveys (42 each year). All plots were surveyed three to four times each year according to time constraints. I captured a total of 75 rails: 12 (10 – year one, 2 – year two) black rails and 63 yellow rails (46, 17). In 2017, I captured the highest number of black rails (6) in the CLC-51 plot and the highest number of yellow rails (16) in the SCS-15 plot (Figure 4-2). For the second year of the study, each plot had increased by 12 MPB as can be seen in the naming convention, however, two plots (SE-76, WMC-84) were burned in a wildfire that occurred three months before year-two surveys began and subsequently decreased to 3 MPB. In 2018, I captured both black rails in SCS-27, and the most yellow rails (11) in the CF-23 plot (Figure 4-3). No rails were captured in the two plots that were set back to 3 MPB, or in the CLC-63 plot in 2018, which was where most black rails were captured in the previous year. In 2017, I recaptured two black rails and six yellow rails, however two of the yellow rails were recaptured multiple times for a total of nine yellow rail recaptures. One yellow rail banded in 2017 was recaptured twice and another was first banded outside of this study in 2016 and recaptured three times in 2017. There was only one recapture of a yellow rail in

2018. Recaptures of birds of both species were in the same plot in which they were

banded.
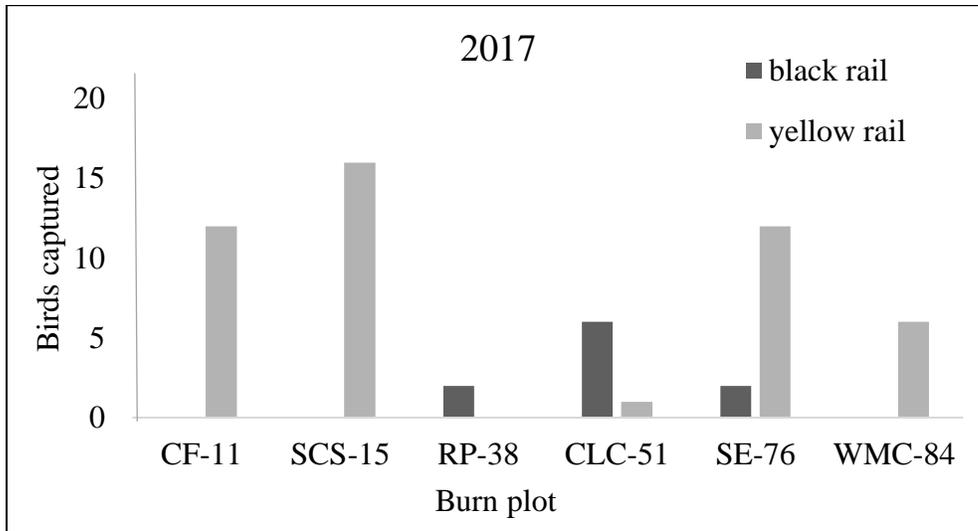
Figure 4-2 Numbers of black rails and yellow rails captured in winter 2017 in six study plots at San Bernard National Wildlife Refuge, Texas, that differed in number of months since last burned. Letter designation is for plot location and number after dash is number of months since the plot was last burned.
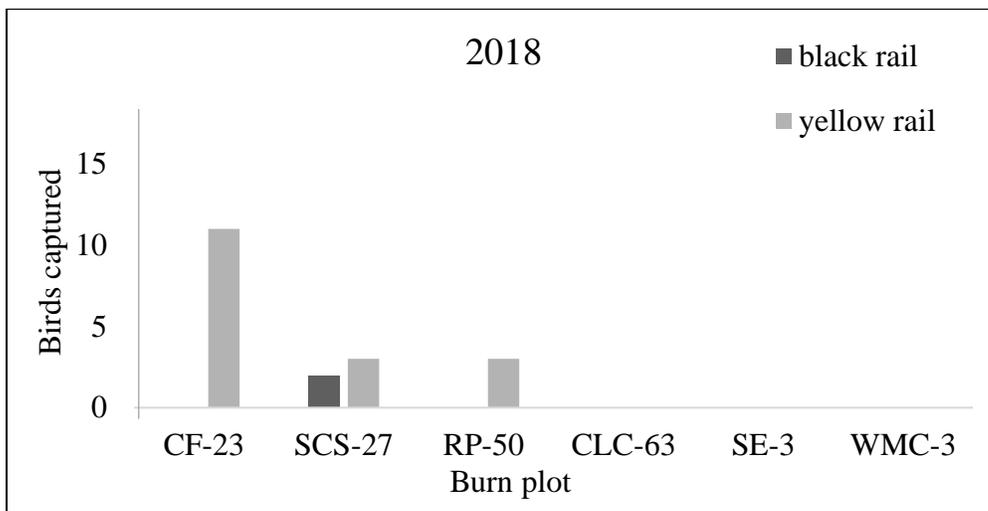
Figure 4-3 Numbers of black rails and yellow rails captured in winter 2018 in six study plots at San Bernard National Wildlife Refuge, Texas, that differed in number of months since last burned. Letter designation is for plot location and number after dash is number of months since the plot was last burned.

Habitat assessment. Dominant vegetation was the same across years and plots (Table 4-1). Gulf cordgrass (*S. spartinae*) was the dominant plant species in each plot, and sea-oxeye daisy was the second dominant in three plots. Eastern baccharis and marshhay cordgrass (*S. patens*) were the second most dominant plants in one plot each. The WMC-84 plot consisted of a mix of grasses and forbs and there was no second dominant plant species. Plots displayed more variability in herbaceous density among than within burn-plots (ICC = 0.65), however, there was no linear relationship between MPB and herbaceous density ($\hat{\beta} = 0.09$, SE = 0.10, $P > 0.05$). Woody frequency also varied among plots (ICC = 0.75) and there was a positive, linear relationship with MPB ($\hat{\beta} = 1.37$, SE = 0.28, $P < 0.001$). Density of RIFA mounds varied more within plots than among plots (ICC = 0.14) but there was no relationship with MPB ($\hat{\beta} = 0.02$, SE = 0.05, $P > 0.05$). Survey-specific averages for habitat variables used as covariates are provided in Table 4-2.

Table 4-1 Dominant plant species in plots differing in months post-burn (MPB) where black rails and yellow rails were captured in 2017 and 2018, at San Bernard National Wildlife Refuge, Texas.

Burn plot	Dominant species 1	Dominant species 2
Crawfish (CF) 11 to 23 MPB	*Spartina spartinae*	*Baccharis halimifolia*
Sargent Checkstation (SCS) 15 to 27 MPB	*Spartina spartinae*	*Borrichia frutescens*
Rail Pond (RP) 38 to 50 MPB	*Spartina spartinae*	*Borrichia frutescens*

Cedar Lake Creek (CLC) 51 to 63 MPB	*Spartina spartinae*	*Spartina patens*
Sargent East (SE) 76 to 3 MPB	*Spartina spartinae*	*Borrichia frutescens*
Williamson McCormick (WMC) >84 to 3 MPB	*Spartina spartinae*	none

Table 4-2 Mean values and standard errors of habitat measurements taken in plots differing in months post-burn (MPB) where black rails and yellow rails were captured in 2017 and 2018, at San Bernard National Wildlife Refuge, Texas. No birds were captured in plots that were three months since burned and hence not included in the statistical analyses.

Survey year	Burn plot	Months since burned	Robel		Woody		RIFA		Overhead cover	
2017										
	Crawfish	11	3.77	(0.06)	3.12	(0.59)	0.98	(0.15)	9.60	(0.07)
	Sargent Checkstation	15	3.52	(0.06)	0.03	(0.01)	0.04	(0.02)	9.00	(0.07)
	Rail Pond	38	7.02	(0.33)	0.05	(0.04)	0.25	(0.18)	10.00	(0)
	Cedar Lake Creek	51	6.07	(0.12)	0.04	(0.02)	0.23	(0.07)	10.00	(0)
	Sargent East	76	4.98	(0.1)	0.39	(0.09)	0.44	(0.07)	9.86	(0.04)
	Williamson McCormick	84	5.97	(0.22)	0.61	(0.18)	0.50	(0.12)	9.80	(0.09)
2018										
	Crawfish	23	3.72	(0.11)	5.43	(0.54)	0.74	(0.1)	9.91	(0.04)
	Sargent Checkstation	27	3.92	(0.21)	1.11	(0.28)	0.57	(0.15)	9.50	(0.15)
	Rail Pond	50	6.32	(0.24)	0.31	(0.16)	0.07	(0.06)	9.83	(0.11)
	Cedar Lake Creek	63	6.06	(0.34)	0.09	(0.31)	0.06	(0.06)	10.00	(0)
	Sargent East	3	1.78	(0.14)	0.58	(0.37)	0.56	(0.12)	6.31	(0.29)
	Williamson McCormick	3	0.69	(0.04)	0.20	(0.12)	1.00	(0.16)	7.06	(0.31)

Model selection. The AIC_c analysis of the candidate models showed bird density was not explained well by any habitat predictor for black rails (Table 4-3)The model featuring woody frequency was a competing model ($\Delta AIC_c < 2$), nonetheless I selected the simpler, null model due to parsimony and since fit was similar [37]. For yellow rails, the model featuring Robel (herbaceous density) best explained differences in the species' density among plots ($\hat{\beta} = -0.59$, SE $= 0.18$, $Z = -3.22$, $P = 0.001$). The summed weights for each covariate across all black rail models, and thus relative importance of each covariate, were: wood $= 0.26$, MPB $= 0.11$, Robel $= 0.10$, RIFA $= 0.07$. For yellow rail models, the summed weights for each covariate were: Robel $= 0.81$, MPB $= 0.09$, wood $= 0.05$, and RIFA $= 0.04$.

Table 4-3 Candidate models examining density of black rails and yellow rails in relation to average woody frequency (wood), mean Robel pole readings (Robel), red imported fire ant mounds (RIFA), and years-post-burn (MPB), in study plots ($n = 9$) located at San Bernard National Wildlife Refuge, Texas, winter 2017 and 2018. The number of parameters in the model is K, AIC_c is Akaike's Information Criterion adjusted for small sample size, ΔAIC_c is the difference in AIC_c value relative to the top model, and w_i is the AIC_c weight.

Model	K	ΔAIC_c	w_i	Log-likelihood
Black Rail				
Intercept only	2	0	0.49	-14.41
wood	3	1.60	0.22	-12.81
MPB	3	3.23	0.10	-13.63
Robel	3	3.37	0.09	-13.69
RIFA	3	4.21	0.06	-14.11
RIFA + wood	4	6.05	0.02	-11.43
wood + MPB	4	8.50	0.01	-12.66
Robel + wood	4	8.73	0.01	-12.77
Robel + MPB	4	10.12	0.00	-13.47
RIFA + MPB	4	10.21	0.00	-13.51
RIFA + Robel	4	10.54	0.00	-13.68
RIFA + wood + MPB	5	17.02	0.00	-10.92
RIFA + Robel + wood	5	18.03	0.00	-11.42

Robel + wood + MPB	5	20.50	0.00	-12.66
RIFA + Robel + MPB	5	22.07	0.00	-13.45
RIFA + Robel + wood + MPB	6	41.02	0.00	-10.92
Yellow Rail				
Robel	3	0	0.71	-23.64
Intercept only	2	3.54	0.12	-27.81
Robel + MPB	4	4.94	0.06	-22.51
wood	3	6.70	0.03	-26.99
MPB	3	6.89	0.02	-27.09
Robel + wood	4	7.16	0.02	-23.62
RIFA + Robel	4	7.19	0.02	-23.63
RIFA	3	7.20	0.02	-27.24
wood + MPB	4	13.37	0.00	-26.73
RIFA + MPB	4	13.56	0.00	-26.82
RIFA + wood	4	13.87	0.00	-26.98
Robel + wood + MPB	5	16.92	0.00	-22.50
RIFA + Robel + MPB	5	16.93	0.00	-22.50
RIFA + Robel + wood	5	19.16	0.00	-23.62
RIFA + wood + MPB	5	25.34	0.00	-26.71
RIFA + Robel + wood + MPB	6	40.92	0.00	-22.50

Discussion

At SBNWR in 2017–2018, wintering black rails were found in plots that ranged in MPB from 27 to 76, and yellow rails were detected in plots from 11 to >84 MPB. There was no correlation between density of either rail species and MPB. There was also no correlation between herbaceous density in the plots and MPB, which may explain the lack of correlation between bird density and MPB. The herbaceous density in the different burn-plots did not increase in equal amounts for every MPB indicating unequal growth rates among plots. Additionally, there was a positive relationship between woody frequency and MPB, and the ICC of >0.50 indicated that woody frequency variation in response to fire was different among plots. Since fire intensity may have varied among

burns and fire interacts synergistically with nutrient availability and hydrology [38], it

follows that the response of the plant communities was not identical in each plot. Despite

the lack of correlation between herbaceous density and bird density, since both rail

species are known for their preference for densely vegetated habitats [12,13], each plot >11

MPB ostensibly exhibited dense enough cover to support yellow rails and plots >27 MPB

had sufficient cover for black rails.

No black rails were detected in either of the plots that were less than two years

post-burn, likely signifying insufficient cover. Studies are sparse on the effects of fire on

black rails, but indications in other regions where cattails (*Typha* spp.) and spikerush

(*Eleocharis* spp.) are the dominant vegetation are that at least one year post-burn is

sufficient for the species, as long as other management practices, such as haying, are not

also occurring [25,28]. An important consideration is comparing these studies is that cattail

marshes regenerate quickly after fire [39,40] and may not require as long a burn return

interval as gulf cordgrass for black rails to resume use. In *Spartina* dominated marshes at

SBNWR, it is likely that ≥2 years post-burn, depending on site-specific regrowth rate, is

necessary for black rails to resume use.

While I captured the most yellow rails in a 15 MPB plot ($n = 16$), I also captured

a large amount in a 76 MPB plot ($n = 11$). Results from previous studies indicate yellow

rails will use areas within a wide range of MPB during breeding [8,23,41], however, studies

conducted on winter grounds in pine savannas along the Gulf Coast found yellow rail

yellow rail abundance decreased with time since fire [22] and occurrence was greatest at <2

years post-burn [9]. These differences in time until use may be in part due to variation in

return interval of fire disturbance among different plant communities throughout the species' range. Yellow rails were detected in nearly every plot >1-year post-burn, suggesting a complex and nonlinear dynamic between years post-burn and habitat features in marshes at SBNWR. Since each plot responded to fire in a different way, number of MBP was somewhat subjective.

The density of black rails was not explained well by any model. Since the sample size was relatively small ($n = 12$), it is possible that the data contained relatively little information, and thus was unable to provide much insight. Though not selected as the best model, woody frequency might have a complex relationship with black rail abundance. Eastern baccharis was the only woody species documented during habitat surveys. This deciduous shrub can grow up to 3 m in height but was rarely taller than 1.5 m in burn plots. Over the course of this study multiple black rails were incidentally detected outside of plot surveys in clumps of eastern baccharis. While it uncertain if there was a structural characteristic of eastern baccharis that black rails found unfavorable in burn plots, indirect effects of the woody shrub seem more likely. For example, woody vegetation in grasslands can impact food resources, alter predator communities, and change hydrology [38,42,43].

Yellow rail density was influenced by herbaceous vegetation density where plots with lower herbaceous density provided more attractive conditions for yellow rails. Previous studies on winter grounds indicate a negative relationship between yellow rail presence and time since fire [9,22], however these studies do not relate yellow rail presence to herbaceous vegetation density post-burn. Similarly, amount of woody frequency was

not found to influence occupancy of yellow rails overwintering in pine savannas of the Gulf Coast [9]. Conversely, studies conducted on breeding grounds have reported a negative association between yellow rails and encroachment of woody plants [23,41]. This may signify that yellow rails are more tolerant of woody frequency on winter grounds than during breeding.

Wintering black rails and yellow rails were found in some of the same burn-plots. Over both years combined, yellow rails were captured in each plot, but black rails were only captured in four of the six plots. There are a few possible explanations for differences in density of rail species across plots. One possible explanation for detecting differences in densities between species is differences in detectability between the species. It is possible that yellow rails will flush more readily upon being disturbed by the bottle-line whereas black rails are more reluctant to fly and instead remain on the ground and run away. There were two instances where I heard black rails calling from within study plots during the daytime outside of surveys, but never flushed or captured a black rail in the same plots at night. However, those birds may have moved out of the plot prior to bottle-line surveys. The other possibility for the disparity in numbers between species across plots is higher abundance of yellow rails in general. Additionally, yellow rails overwintering on Anahuac National Wildlife Refuge in Chambers county, Texas, were found to be gregarious and non-territorial [44]. A clumped distribution of yellow rails within the burn-plots may have helped facilitate more detections of the species. If black rails exhibit a higher degree of territoriality, there would be less birds per unit area requiring expanded survey efforts to detect numbers equal to yellow rail detections. The

nature of black rail territoriality is poorly known [12] however results from the radio telemetry study I conducted concurrently with this study suggest black rails are territorial in winter in Texas. Black rails responded to play-back of conspecific calls with aggressive calls ("grrr" vocalization) and 95% minimum convex polygons did not overlap. Overall, I detected markedly more yellow rails ($n = 65$) than black rails ($n = 12$). This was likely due to higher abundance of yellow rails but I speculate that it is also in part due to black rails being less detectable or low effectiveness of the bottle-line method of capture.

In many instances both rail species were found together in the same plots, however in uneven ratios. Previous studies have found intra- and interspecific competition occurring between wintering and resident birds [45-47] and with increasing climate change, many of these relationships are being altered [48,49]. Other studies have found migrants to be more flexible in foraging behavior which facilitates coexistence [50]. In the Sierra Nevada foothills of California, occupancy for the co-occurring black and Virginia rail was strongly positively correlated, especially in smaller marshes, demonstrating a lack of competitive exclusion [51]. These species are morphometrically dissimilar and coexistence may be maintained by resource partitioning on a microhabitat level [52]. Yellow rails and black rails have similar morphometrics such as mass, bill size, and tarsus length. The species also have similar diets and are known to share some of the same wintering grounds in Texas, thus it is possible that exploitation or interference competition occurs since many plots had much higher numbers of yellow rails than black rails. In exploitation competition, individuals use the same resources without interfering

with (and sometimes without even encountering) one another but resources are reduced simply because both species are exploiting them. In interference competition, a behavioral component is usually involved, an example being aggression of one species reducing another species' access to a resource [53]. Acting mainly through resources, interspecific competition may reduce fitness and limit the abundance and distribution of birds [53,54]. More in-depth studies are necessary to better understand the competitive relationship between these two rails.

I captured a substantially lower number of rails in the second season ($n = 19$) compared to season one ($n = 57$). Wildfire consumed two of the burn plots on 17 October 2017, just three months before the second season of the study began and subsequently no birds were found in those two plots. The low amount of cover provided by new growth was evidently not sufficient for either rail species to occupy either of these plots. There were also lower numbers of birds during the second season in plots that were not affected by the wildfire, for instance the CLC-4/CLC-5 (Cedar Lake Creek) plot. During the first year, seven birds were captured in this plot, six of which were black rails, and no birds the second year. Besides the wildfire occurring between seasons, Hurricane Harvey made landfall on the gulf coast of Texas on 25 August 2017 just south of SBNWR before becoming a tropical storm and making its way up the coast. Tropical Storm Harvey caused substantial flooding on the refuge, including in the Cedar Lake Creek unit, that remained well into September (J. Wilson and J. Woodrow, personal communication). Both species of rails have been found to prefer moderate water levels that are not too deep [8,12]. It is possible the rails avoided areas inundated with substantial levels of

standing water for instance the Cedar Lake Creek unit and established winter territories elsewhere.

The water had receded from the Cedar Lake Creek unit before surveys began, however hurricanes can significantly impact bird populations over an extended period due to loss of resources like fruits, seeds, and insects. Waide [55] found a reduced number of arthropods in the stomach of birds following a hurricane. The storm-induced standing water in the Cedar Lake Creek unit may have negatively impacted prey populations (e.g. gastropods and arthropods) and thus reduced suitability of the plot. Some grassland bird species exhibit low site fidelity on winter and breeding grounds as an adaptation to habitat fluctuations and annual variation [56,57]. During the second year, rails may have selected areas outside of the study plots in response fluctuation in resources between years. Additionally, the vegetation in this plot was exceedingly tall and thick. The canopy of grass may have been dense enough to impede the ability of birds on the ground to quickly escape the matted grass and flush. Birds may have preferentially fled on foot thus never revealing themselves to surveyors. I suspect there is some heterogeneity in detection rates across the different burn regimes due to differences in vegetation structure and variation in behavioral response of the birds.

The bottle-line method of capture is ostensibly the most effective low-impact method used to capture these two secretive rails. Nonetheless, recapture rates indicate that the bottle-line method is still not very effective for capturing birds. Combining capture results from both species, recapture rate the first year was 16.5% and 5.2% the

second year. It is likely that bird density was greater in each plot but we missed many individuals.

Interestingly, each recapture occurred in the same plot as the original capture. This includes within season and across years for the inimitable yellow rail captured four times across two years. Another study within the TMC reported within-year recaptures of yellow rails as sufficiently common indicating a high degree of winter site fidelity [6]. Within season and annual site fidelity has been documented in many avian species and is thought to be an indication of plentiful or stable resources [57-59]. Virginia rails in Arizona occupied the same breeding area for three consecutive years [60], however little if anything else is known about site fidelity in rails.

Overall, I found no strong or definite habitat associations between black rails and the burn-plots at SBNWR. There may have been other habitat attributes that I did not measure that show definite relationships, for instance food supply. Although water level has been found to be an important factor for both black rails and yellow rails [8,61-63], measurable amounts of surface water was rarely seen in study plots. Furthermore, a telemetry study conducted at the TMC indicated yellow rails did not move to new locations after areas dried out [6]. At SBNWR, yellow rails seem to tolerate a relatively wide range of burn regimes but are more tolerant of habitats with lower densities of herbaceous cover. Black rails and yellow rails appear to have different preference for vegetative structure, and therefore management directed at one may not benefit the other. At SBNWR, designing burn regimes to maintain a mosaic of seral stages may be the best management strategy for black rails and yellow rails.

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CHAPTER 5

CONCLUSIONS

In the preceding chapters I provided baseline data to aid in the assessment of the resiliency and redundancy of the eastern black rail in coastal Texas. This type of information is critical to the overall evaluation and assessment of a species' status. To accomplish this, I conducted three separate field studies to build a foundation of biological information for the species in Texas and try to understand what influences the species' distribution at multiple scales in coastal Texas. The data collected during my field studies fills in some of the basic life history information for black rails that has been missing for the state.

In Chapter 2, I examine drivers of distribution at the landscape-level of the Texas coast. I provided an overview of large-scale black rail surveys which I conducted over 2 spring seasons at five sites along the Texas coast. I combined occupancy data collected during repeat surveys with GIS data and fit occupancy models. With the resulting top occupancy model, I created a species distribution map in GIS to identify areas of suitable habitat along the Texas coast. Highest predicted occupancy probabilities were in high-marsh habitats containing high levels of herbaceous vegetative cover, especially that of gulf cordgrass. I found positive associations between black rail occurrence and average annual precipitation indicating that in coastal Texas, distribution of black rails is limited not only by dense herbaceous cordgrass cover, but possibly by precipitation as well. A very small portion of the study area (5.4%) was predicted to have an occupancy

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probability for the species above 40%, exemplifying the need to protect and proliferate habitat that contains known black rail populations in the state. The predictive map I created can be used as a guide for where to focus survey efforts and potentially lead to the discovery of more black rail populations.

In Chapter 3, I explored winter habitat selection at a home range scale through the use of radio telemetry. Black rails in coastal Texas during winter had smaller home ranges than those found in Florida during breeding. Seasonal variation in home range size has been documented in other Rallids however winter range is usually larger than breeding range. A smaller home range in Texas may be indicative of regional habitat differences or density-dependent variables such as population size. Gulf cordgrass was found to be an important feature within home ranges, as well as areas of high-marsh. The low-tidal marsh was used proportionally less than its availability. Black rail home ranges included gently sloping topography suggesting the importance of having easy access to higher ground on-foot. During radio tracking, I discovered a black rail nest and report the earliest known nesting date for the species.

Finally, for Chapter 4 I investigated what influences distribution within habitat associations. In this study I examined density relationships of black rails in the context of fire, an important marsh management tool commonly used in black rail habitats. This study also included the closely related yellow rail which shares wintering habitat with black rails. I estimated densities of each species as a response to habitat features in study plots that differed in time since burned. Results showed both species will use habitats within a wide range of burn regimes. There was no correlation between months post-burn

and density of either species of rail, however it seems there are minimum cover requirements. Black rails appear to require ≥27 months post-burn and yellow rails: ≥11 months. I found no strong relationships between habitat features measured in burn plots and black rails, while plots with lower herbaceous density were more attractive to yellow rails. Both species were found using the same plots at times however they may not prefer the same vegetative structure, implicating the importance of maintaining a mosaic of seral stages.

Collectively, these studies provide baseline information to help us understand some of the biological needs of black rails in coastal Texas. However, I have merely scratched the surface and much more work is necessary to further our limited understanding of this enigmatic bird. Besides more biological studies, a vital component currently needed is long-term monitoring. Long-term monitoring is easy to implement and is the essence of resiliency assessment. My studies have provided information that is crucial for beginning to understand black rail distribution, and how to manage habitat for the species, in coastal Texas.

Black Rail Literature Review

Introduction

Rallidae is a widely distributed family of long-toed marshbirds that includes coots, rails, soras, gallinules, and crakes. Of the ten species of Rallidae that breed in North America, the black rail (*Laterallus jamaicensis*) is the smallest and often thought of as one of the most elusive birds on the continent. The small body size and particularly shy nature of this rail, coupled with its preferred habitat consisting of the densest of marsh vegetation (frequently beset by hordes of mosquitoes and other flying insects), has made the species extremely difficult to study. Often compared in behavior to that of a mouse [1,2], black rails are reluctant to fly but flee on foot when disturbed and quickly disappear into dense vegetation. Due to their diminutive size, black rails are usually confined to moist soil marshes or those with the shallowest (fresh or salt) water. The narrow habitat characteristics and cryptic behavior of this rail makes well-planned aural surveys as the principal means of reliable population assessment. These surveys include call playback and might be the only effective way to detect black rails without using radio telemetry [3-6].

There are several disjunct breeding populations of black rails in North America including California, Arizona, the Atlantic and Gulf coasts, and numerous inland locations as far north as Minnesota. In Texas, black rails are listed as rare to locally uncommon residents of the upper and central Texas coast [7,8]. Due to their secretive

nature, black rails are often given the designation of "rare and local" throughout much of their range, however some researchers have mentioned they might be abundant than they seem [9-12].

Most research on black rails has been conducted in California, Arizona and Florida [6,13-16]. Black rails are a species of conservation concern in the United States (Arizona Game and Fish Department 2006; California Department of Fish and Game 2006; U.S. Fish and Wildlife Service 2008) and Endangered in Mexico (Diario Oficial de la Federacion 2010). Several states along the Atlantic coast as well as California and Arizona list the bird as endangered or threatened. Although they are listed as a species of highest conservation concern on Audubon's Watchlist and their IUCN conservation status is Near Threated [17], the species has no special protection in Texas and very little is known about the population status and distribution of the black rail in the state. The objective of this literature review was to collect and compile all information pertaining to the black rail in order to examine each source of available baseline data.

History

Formerly referred to as Least Water Hen, Black Crake, Farallon Rail, Little Red-eyed Crake, and Little Black Rail, the species was first described in the United States in 1756 from specimens brought back from Jamaica by Patrick Browne, an Irish physician and botanist [18]. The first published drawing came from Edwards [19] in 1758 in his *Gleanings of Natural History* (Appendix Figure 1) and the bird received its scientific name and technical description in 1788 by Gmelin [20]. Black rails remained relatively obscure for

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the next 50 years due to cryptic behavior, low abundance and disjunct, restricted

distributions. In 1838 Audubon [21] announced in *Ornithological Biography* that the Black

Rail was a bird of the United States (Appendix Figure 2), having been sent specimens

from Philadelphia. For many decades after this announcement, black rails remained

sufficiently rare that mere sight records of the bird were considered worthy of reporting

in publications. Records began surfacing along the east coast from Massachusetts south

along the coast to South Carolina and Florida, and inland to New York and Illinois. The

first black rail nests in the United States were found in New Jersey in 1810 and 1844 [10],

and then Illinois in 1875 [22].

Appendix Figure 1 Plate from Gleanings of Natural History[19] illustrating the "Least Water-Hen", which was the first common name of the black rail.

Appendix Figure 2 Plate CCCXLIX from Ornithological Biography [21] illustrating the "Least Water hen" (*Rallus jamaicensis*). Note: incorrect depiction of leg coloration as discussed by Meanley and Stewart [23]. Legs of black rails are actually a greyish-brown color.

The California black rail subspecies (*L. j. coturniculus,* meaning: "a little quail") was first described in 1874 from a specimen found on the Farallon Islands off the coast of San Francisco [24]. It was thought that this bird was different from the birds on California's mainland so it was deemed a subspecies by Baird, et al. [25]. However, in 1907 Brewster [26] decided it was actually an immature bird from the mainland. Brewster also concluded from specimen comparison that the black rails inhabiting the eastern United States and Jamaica differed from those found in California. In 1923 Coale announced the birds in Jamaica were different than those in the United States and renamed the inland nesting

Eastern black rails *L. j. stoddardi* after a specimen found near Chicago [27,28]. Nevertheless, they are currently considered the same species: *L. j. jamaicensis*.

Most of what is known about Black Rails comes from piecing together information scattered throughout the literature. There are over 100 publications about Black Rails since the late 1800's concerning distributional records or systematics. Nonetheless, the first organized studies of the species were not conducted until the late 1960's and mid 1970's. These came in the form of a master's thesis in Maryland [29] and aural Black Rail surveys conducted in California and Arizona [3,4,30]. This was also when the presence of an inland population of Black Rails in Arizona along the lower Colorado River was confirmed in the literature [4]. In the late 1980's the first Black Rail radio telemetry study examining nesting biology was conducted in Yuba County, Arizona [31].

Distribution

There are five subspecies of Black Rails, two of which breed in North America: the nominate Eastern Black Rail *(L. j. jamaicensis)* and the California Black Rail (*L. j. coturniculus*) (Appendix Figure 3). The California Black Rail as well as an inland population of the Eastern Black Rail in Kansas are geographically separated from Atlantic and Gulf coast populations of Eastern Black Rails (Eastern Black Rail Conservation and Management Working Group 2014).
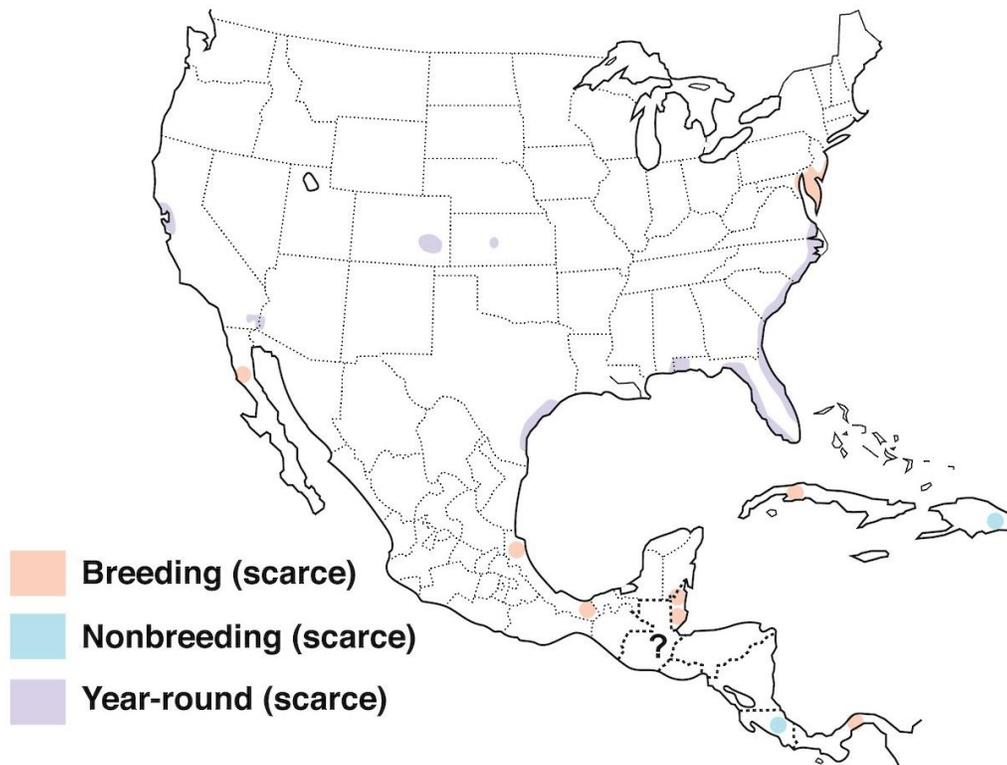
Appendix Figure 3 Distribution of the black rail (*Laterallus jamaicensis*). From Eddleman, et al. [32].

L. j. jamaicensis. The eastern black rail is thought to be at least partially migratory and breeds locally along the Atlantic coast in the eastern United States from Connecticut to south Florida, along the Gulf coast from Florida to the central coast of Texas, and into Central America [32]. Historically, the breeding range may have extended as far north as Massachusetts but contracted south to New York sometime in the early 20th century and today the core breeding range is from New Jersey south along the coast to Florida (Eastern Black Rail Conservation and Management Working Group 2014).

There are sporadic inland records from the Arkansas River marshes in southeastern Colorado - as many as 74 calling birds in recent years [33], Kansas, Arkansas,

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Oklahoma north to Minnesota, and Illinois east to Connecticut. Eastern black rails winter along the Atlantic coast from New Jersey to south Florida, in the vicinity of the Gulf of Mexico (from coastal Texas east to Florida) to Guatemala and the Greater Antilles [34,35]. The online citizen science checklist program eBird.org [36] shows eastern black rail records from 31 states and Canada.

The eastern subspecies also occurs outside of North America at scattered locations in Central America, including east Mexico, Belize, Honduras [37], Costa Rica, Cuba and Jamaica, and possibly Puerto Rico [34]. Once considered a resident of Jamaica, it is probably severely reduced if not extinct now. Extinction in Jamaica might be due to the introduction of the mongoose (*Herpestes javanicus*) in 1923 [38].

L. j. coturniculus. The California black rail is largely resident and occurs in disjunct regions of northern California and southwest USA (southern California and western Arizona), as well as Baja California. More specifically, it breeds in the Sacramento Valley and the San Francisco Bay-Delta Estuary area, various locations south of San Francisco along the Pacific coast, the lower Imperial Valley along the All American Canal, along the lower Colorado River of Arizona and southern California, and in northwestern Baja California in the El Doctor and Cienega de Santa Clara wetlands [32,34,39]. In 1994 it was discovered in the northern Sierra Nevada foothills in Butte, Placer, Nevada, and Yuba Counties [40,41].

Movements

It is believed that inland populations of eastern black rails and those in the northeastern United States migrate to the Atlantic and Gulf coasts, as well as Cuba, Jamaica and Guatemala for the winter. Nevertheless, these populations are poorly understood [32,34,42]. Spring migration occurs from mid-March to early May [34]. Some spring arrival dates in the northeast USA include 10 April (NJ – New Jersey), 12 April (MD - Maryland), and 19 April (NY – New York) [43]. Southward migration occurs from September to mid-October [38,44] with as late as 7 Nov in MD, 1 Nov in NJ, and 29 Oct in NY [42,43]. The California race is seemingly sedentary but is known to disperse widely from breeding areas and sometimes appear in atypical habitats [32].

Black rails migrate at night along a broad front [32] and numerous collisions with man-made objects (utility wires, building and towers) have been documented [45-48].The distribution of collision kills indicates no apparent migration routes [32]

Status

The population of California black rails is estimated at 10,000 – 25,000 individuals (Wetlands International 2012), while the eastern black rail population along the Atlantic and Gulf Coast states my consists of only 455 – 1,315 breeding pairs [49]. Yet, the species is not sampled effectively by the U.S. Geological Services North American Breeding Bird Survey (BBS) since it occurs in isolated wetlands and is rarely detected visually [50,51]. Declines have been documented in the southwestern USA [13] as well as along the east coast where reports in Virginia and Maryland indicate declines of 75% or

greater (Eastern Black Rail Conservation & Management Working Group 2014). Catastrophic decline has been documented within the species' northern reaches which includes a 450 km contraction of the northern range limit, which has moved from Massachusetts south to New Jersey [49].

Black Rails in Texas

Very little is known about the ecology of black rails in Texas. There are Texas records of the species as spring migrants as early as April 1879 [52], however, they were not listed as a bird of Texas until over a century later in 1983 [35]. During the 1987-1992 fieldwork seasons of the Texas Breeding Bird Atlas project, surveyors found one probable and one possible breeding site in the Coastal Prairies region within the central coast. There are records as far west as the High Plains and north in the Panhandle [53]. Along the Texas coast, vocalizing birds in the spring and summer suggest breeding activity [8]. There are nesting records from Oberholser [7] indicating nesting dates of 9 May in Galveston and 5 June at Brazoria NWR.

At the present time (Appendix Figure 4), the birds are considered a "rare migrant" in the eastern third of Texas (east of the Balcones Escarpment) and "rare to locally uncommon" residents on the upper and central coasts [8]. Vocalizing black rails were recorded incidentally by an autonomous recording unit in April of 1995 at Laguna Atascosa NWR [54] and observations on eBird [36] include the lower coast as well. Additionally, there are numerous records from north central Texas [55] the Texas

Panhandle region[36], some occurring during breeding months [53]. These findings suggest the exact distribution of black rails in Texas is unclear.
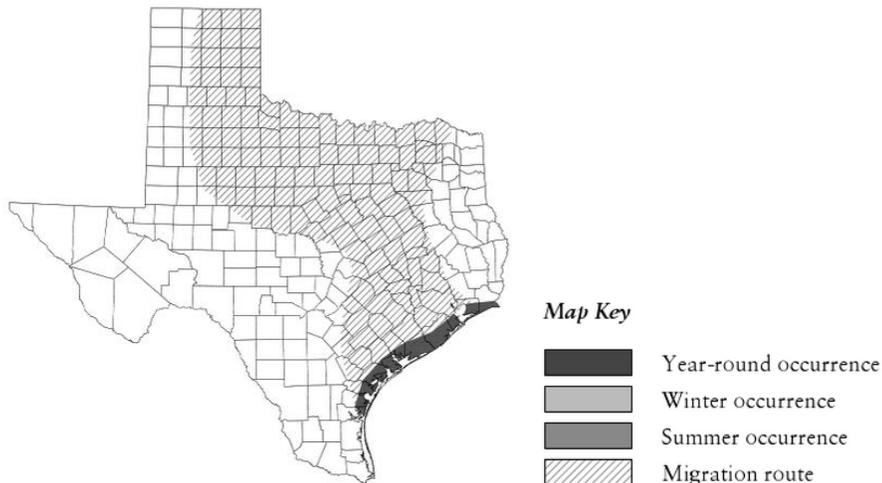
Appendix Figure 4 Distribution of the eastern black rail (*L. j. jamaicensis*) in Texas from Lockwood and Freeman [8].

Physical characteristics

Total length for adult black rails is 12-15 cm, with a wingspan of 22-28 cm. The head is blackish; nape to the upper mantel is chestnut or rufous and the rest of the upperparts and flanks are blackish-brown and finely barred or spotted with white. Immature birds probably have heavier spotting [34]. The bill is black, and legs and feet are flesh to chocolate-brown where immature birds gradually gain the darker color. The bright red irises of adults differentiate black rails from other North American rails. Irises of juveniles transition as the bird ages from shades of brown, to olive, to rufous, then dull orange (Laurie Hall, pers. comm). Sexes are similar in size but sexually dimorphic in

plumage. Females have a pale gray to white throat, and medium to pale gray ventrum while males are darker overall, with a pale to medium gray throat [32,34].

There are some subtle differences between eastern and California black rails. The California black rail is smaller (29 g), has a smaller, slender bill, and is more brightly colored than the eastern subspecies. California black rails have a deeper colored and larger chestnut patch extending down their back, and a chocolate-brown crown [34]. The eastern black rail (35 g), in comparison, has a larger and stouter bill, the chestnut color is confined largely to the nape, and the crown is grayish [32,34].

Habitat

Eastern black rails. Habitat includes the higher reaches of salt, brackish, or fresh water marshes, dominated by fine stemmed plants such as sedges, rushes, and grasses. Habitats tend to include *Spartina patens, S. alternaflora, S. cynosuroides, Distichlis spicata, Juncus roemerianuis, J. gerardi,* pickleweed (*Salicornia* spp.), *Typha* spp. or *Scirpus olneyi* [56]. Habitat can also include dryer upland edges that may include *Iva fructescens* and *Baccharis halimlfolia*, and *Phragmites australis* [7,29,42]. In New Jersey, survey sites where the most black rails were detected were near upland edges of marshes which contained at least some *S. Patens*. These sites were rather dry and were rarely inundated by high tides [56]. Other habitat characteristics include vegetation density, distance to open water, and stability of the water regime [42]. In South Carolina, black rails were positively associated with management impoundments and negatively associates with unmanaged tidal marshes [57].

California black rails. Occur in a variety of habitats including high-marsh along the California coast and freshwater marshes along the lower Colorado River. This subspecies will occupy saltmarshes that flood more frequently than on the east coast but they require adjacent upland vegetation for escape during extreme high tides [32]. They are found associating with plants that are more characteristic of shallow water or moist soil (e.g.: *Schoenoplectus pungens* and *Pluchea sericea*) along the upland/wetland interface [13]. Commonly reported plant associations include *Salicornia*, *Scirpus, Juncus, Grindelia, Distichlis,* and *Typha* to a lesser degree [4,6,30,58]. Highest abundances detected during surveys in the San Francisco Bay Estuary were at marshes with unrestricted tidal flow [6,30], possibly due to higher food resource levels in tidal marshes as opposed to diked marshes. Yet, inland populations (lower Colorado River) select sites with shallow, stable water levels [4,6]. Nadeau and Conway [16] experimentally tested black rail water-depth preferences and found it ranged from saturated soil to 100 mm of water. Previous studies report preferred water levels at ≤3 cm [14,59] which corresponds to the bird's tarsal length of $\bar{x} = 2.5$ cm.

Black rails in the Sierra Nevada Foothills occur in small, irrigation-fed wetlands averaging only 1.3 ha in area (0.01 ha was the smallest [41]), whereas all other populations in the USA typically inhabit marshes >50 ha [4,6,58]. Flores and Eddleman [14] found that use of habitat differed between age and sex classes during all seasons, especially in winter where males were found in dryer sites with denser vegetation closer to upland vegetation compared to females. Richmond, et al. [60] found that large (>5 ha) irrigated marshes with a nearby occupied neighboring marsh were most likely to be occupied.

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Overall, black rails seem to prefer high marsh habitats that are well-drained with only moist surfaces or very little standing water (up to 100 ml) and the marsh may be fresh, salt, or brackish. Dense vegetation is preferred and structure is more important than exact species composition [14,59]. Including a gradual slope at the upland-wetland interface would allow Black Rails to easily track their preferred water depths [16]. Maintaining a shallow, stable water regime and a plant community of dense, fine-stemmed (e.g.: *Spartina, Schoenoplectus, Scirpus, Salicornia*) species are some of the key components of managing habitat for black rails.

Diet

The diet of black rails consists mainly of small (<1cm) aquatic and terrestrial invertebrates, including snails, amphipods, isopods, spiders, ants, grasshoppers, earwigs and beetles [32]. Also seeds of aquatic vegetation (*Typha* and *Scirpus)* are taken but more so in the winter when less animal foods are available Ehrlich [32,61]. The roofs of black rail's mouths contain a number of fleshy, pointy, bumps that protrude posteriorly and presumable function as barbs to aid in holding on to captured prey [29].

Behavior

Black rails do not readily flush; instead the birds prefer to run and hide and are frequently compared to a mouse [2,29,62]. Weske [29] found black rails were much harder to flush during the day then at night. Birds only seemed to flush when there was no escape route available on foot. When birds do flush, it's usually a short, weak flight, sometimes

described as boomerang-like with dangling legs [63,64]. Over long distances such as during migrations, however, the flight is fast and strong [34].

When disturbed in marshes, black rails usually became silent for a period of time [29]. Weske [29] also thought birds were shyer or more difficult to detect under bright moonlight conditions. Spear, et al. [65], however, found that detections of black rails increased with increased moonlight. Weske [29] believed black rails spent all evening singing, restricting foraging to daytime and crepuscular times (i.e., dusk and dawn). Conversely, telemetry studies in Florida found black rails to be active throughout daylight hours when not incubating eggs and inactive at night [66].

Black rails may display strong site fidelity under certain conditions. Within larger, more stable marshes in the San Francisco Bay, Tsao, et al. [59] reported that birds may frequently move between closely spaced (500 m apart on average) smaller marshes. This pattern was also described for black rails in the Sierra Nevada Foothills [67].

Vocalizations

The most commonly heard black rail song is seemingly the advertising call: *kik-kik-kerr* or *kee-kee-do*. The number of "*kee*" notes vary and calls are usually repeated every 3-6 seconds. Birds may call very fast or very slow and incessantly for hours [42]. The conventional thinking was that only males made the advertising call. A study in Florida, however, documented females making the advertising call, nevertheless, females made the advertising call less frequently than males [15]. Furthermore, females vocalized less often than males in general [15]. Females were also reported to make a *coo-coo-coo* like

that of the yellow-billed cuckoo (*Coccyzus americanus*) or least bittern (*Ixobrychus exilis*) [56,68-70]. Other vocalizations include *churt* and *growl*. After attempting to capture black rails with the aid of call playback, a type of contact call between adults and chicks, best described as a repeated *chew-chew-chew*, was also documented (personal observation).

Nesting

Nests have been found in fresh and salt wet meadows [71,72], in short and tall grass, and in dense stands of *Salicornia, Typha,* and sedges [31,63,73]. Nests in tidal marshes with mesic to hydric soils are usually in the highest sections that are only flooded by the highest tides [38]. Nests are a loosely woven cup constructed in dense vegetation and usually just a few centimeters above ground level [31]. But there is variation in nest placement. Sometimes nests may be up to 46 cm off the substrate [34], sometimes over shallow (<3cm) water, and sometimes supported by a mat of last year's vegetation [71]. Carleton, et al. [73] on Long Island reported: "the nest was in fairly short grass with a few scattered rushes, near the edge of a salt marsh, though the nest itself was on the ground where it was dry". Black rails in Florida preferred sites near saltpans where they built nests over mud or moist soil in dense herbaceous vegetation, at a mean height of 6 cm over the ground [66]. Similar mean nest height was reported in Arizona [31].

Nest material include dead and living surrounding vegetation (e.g. *Salicorina*, *Spartina*, *Typha*, *Eleocharis*), often covered by a dome of grass, and sometimes including a ramp of dead grass leading from an opening in the side of the nest to the ground

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[12,31,34,42]. In Florida, nests were constructed of living and dead material and were located either in a dense clump of vegetation that hid the nest from above or domed with one side entrance [66]. Female *L. j. jamaicensis* will lay 4-13 eggs, while *L. j. coturniculus* usually lay 3-8 eggs, probably at daily intervals [34]. Eggs are buffy-white, with fine brown dots [34]. Incubation is performed by both sexes and lasts about 10-16 days [61]. Chicks hatch synchronously and are semi-precocial, leaving the nest within 24 hours but continuing to be fed by parents for an undetermined length of time [61].

Threats

Predation and invasive species. In coastal areas subject to tidal influence in California, high tides have been known to inundate black rail nests causing the eggs to float away [63] Ingersoll [64] and cause some adults to temporarily leave the cover of the marsh during the winter [30,74]. During high tide in the San Francisco Bay, Evens and Page [75] witnessed two predation events on black rails when northern harriers (*Circus cyaneus*) caught birds that remained in the marsh after high tide inundation. They also observed great egrets (*Casmerodius albus*) capture 15 black rails and great blue herons (*Ardea Herodias*) capture 2 black rails during high tides in a salt marsh at Tomales Bay, California. Some of these birds, however, were able to escape capture and flee into emergent vegetation 20 – 30m away. Additionally, four radio-tagged California black rails were depredated during high-tide events in the San Francisco Bay area [59].

Other predators include great-horned owls (*Bubo virginianus*), short-eared owls (*Asio flammeus*), ring-billed gulls (*Larus delawarensis*), domestic cats, and possibly

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loggerhead shrikes (*Lanius ludovicianus*) [75-78]. Vegetation around the periphery of marshes may mitigate depredation by avian predators during high tides by providing alternate cover [75].

Since black rails are ground inhabiting birds and also make their nests at ground level, nests and individuals may be subject to numerous predation threats. At St. Johns River marsh in Florida, one hatching chick was killed and partially eaten by red fire ants (*Solenopsis* sp. [32]). Predation by others including snakes, rats, *Vulpes vulpes*, snapping turtles and various mesocarnivores, is likely, although undocumented [34,42].

Angradi, et al. [79] found lower abundance and diversity of macroinvertebrates in marshes dominated by the invasive *Phragmites* compared to marshes consisting primarily of native *Spartina* cordgrasses. Nevertheless, *Phragmites* has been present at the sole black rail breeding site in New York since 1950 indicating they are tolerant to the plant [80]. In New York, black rails were found in pure stands of Phragmites and into the wetter, *S. alterniflora* zone of the marsh [68].

Egg predation by hogs (*Sus scrofa*) and habitat degradation via goats (*Capra hircus*) and invasive woody plants threatened the persistence of the endemic Galapagos rail (*Laterallus spilonotus*) populations [81]. Estimated population density of this closely related rail increased by over an order of magnitude after the eradication of feral hogs and goats [81]. According to Texas Parks and Wildlife Department, there is currently an estimated population in excess of 1.5 million feral hogs in Texas. Although there is no

documentation of direct predation of black rails by feral hogs, the hogs can degrade large areas of wetland habitat while rooting [82].

Severe weather. Strong winds or low cloud ceilings could possibly increase collisions with man-made objects (towers and buildings) [46,83] or lead migrants to land in hostile environments [84]. If nesting areas become flooded by abnormally high water levels, this could reduce reproduction and perhaps invertebrate prey as well [38,85]. Drought could also reduce invertebrate prey base. Seasonality may affect invertebrate availability. Flores and Eddleman [86] found lower biomass of invertebrates trapped at the sites used by black rails and mean weight of the birds was lower during the fall and spring seasons.

Cattle grazing. Light to moderate grazing at irrigated marshes had no effect on black rail occupancy but had negative impacts at non-irrigated marshes [60].

Habitat loss & climate change. The single greatest threat to black rail is the loss and degradation of its habitat whether attributed to human activity or natural events such as hurricanes and drought [38,56,87]. Marsh subsidence (sinking of ground level) is caused by groundwater removal, diking of salt marshes, water level fluctuations, and wildfire [30,38]. Since black rails are very sensitive to water levels, mitigation of subsidence may be important. Other contributors to marsh habitat loss as well as degradation of marsh due to land-use practices include salt production, urbanization, and agriculture practices. Habitat loss also includes loss of transition zones between marsh and upland due to diking and cattle grazing [6].

Sea level rise could force black rails out of their normal habitats to upland areas, which are typically more marginal habitats [88]. If marsh transgression upslope is inhibited by barriers like agriculture fields, roads, or urban or private property, local extirpation could occur. Warmer sea-surface temperatures have caused an increase in frequency and intensity of hurricanes since 1970 [89,90] posing significant threats to coastal areas including storm surges, extreme winds, and sustained rains. Additionally, greater inundation frequency and water depth during tidal events could increase predation events and reduce nesting success if nests become inundated. Black rails are forecasted to suffer potential reductions of 90-99% of their Chesapeake Bay breeding habitats over the next 90 years (The Center for Conservation Biology 2014).

Contaminants. A considerable portion of the threatened California black rails at the San Francisco Bay estuaries may be at risk of negative reproductive effects due to methylmercury contamination [91]. More than 80% of the western subspecies inhabit the San Francisco Bay estuaries year-round. Pesticides leached into wetlands from nearby agriculture fields or applied directly to saltmarshes may contaminate black rails, although there is no documentation of this. Ingestion of lead shot has been documented in the closely related sora (*Porzana carolina*) [92].

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