ABSTRACT

ROGERS, SAMANTHA L. King Rail (*Rallus elegans*) Occupancy, Reproductive Activity and Success in Fire Managed Coastal Marshes of North Carolina and Virginia. (Under the direction of Jaime A. Collazo, Ph.D.).

King Rails (*Rallus elegans*) are secretive marsh birds that are experiencing range-wide declines due to loss of freshwater emergent wetlands. Prescribed burning is often utilized to manage the remaining marsh habitat for wildlife. This study examines the influence of prescribed burns on the probabilities of occupancy and reproductive activity by King Rails in coastal North Carolina and Virginia marshes. I categorized survey plots by fire history: recently burned plots were burned the same or previous year (0-1 YSB), and non-recently burned plots were burned two or more years prior ($\geq$2 YSB). I measured vegetation richness, horizontal and vertical cover at survey plots and nest sites to test for differences in microhabitat, and continuously monitored nests using video surveillance to describe parental behavior and determine nest fate. The probabilities of site occupancy and reproductive activity were greater in recently burned marsh plots than non-recently burned marsh plots. King Rails nested disproportionately in recently burned marshes, and nest survival was negatively influenced by the duration that nests were left unattended. Confirmed predators included raccoon (*Procyon lotor*) and black rat snake (*Elaphe obsoleta obsoleta*). Evidence supported a positive response to prescribed burns; however, the lack of microhabitat differences between burn categories suggested that the response was mediated by other factors affecting habitat quality, such as food availability. This study connected regional and population objectives at the management unit level by addressing current management actions and King Rail responses to those actions that are related to fitness. I recommend that the influence of prescribed burn on demographic parameters, especially nest success and brood survival, be assessed in a similar fashion at other management units before results are generalized and used to inform management decisions.

King Rail (*Rallus elegans*) Occupancy, Reproductive Activity and Success in Fire Managed Coastal Marshes of North Carolina and Virginia

by
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BIOGRAPHY

Samantha Layne Rogers is originally from in Midlothian, Virginia. She graduated summa cum laude from Virginia Commonwealth University in 2008 with a Bachelor of Science in Biology and a minor in Chemistry. During her undergraduate study, coursework expanded her love of learning about the natural world to include a new interest in ornithology. She decided to pursue this interest in a research-oriented program in Zoology at North Carolina State University. Following the completion of her Master's degree, she plans to continue her career in ecological research.

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Occupancy and abundance of King Rails in managed coastal marshes of North Carolina and Virginia

1.1 Abstract

King Rails (*Rallus elegans*) are secretive marsh birds that primarily occupy freshwater marshes with emergent vegetation and shallow water. Their populations have experienced range-wide declines since the 1960s. Curbing declining trends requires a greater understanding of their ecology and response to management practices in freshwater marsh habitat. Management practices include prescribed burns to limit the growth of trees and shrubs and remove dead vegetation. My objectives were to estimate occupancy and abundance of King Rails at Back Bay and Mackay Island National Wildlife Refuges (NWR), and determine how these parameters were influenced by fire management history. I surveyed 41 plots from 27 April 2010 to 28 June 2010. Fifteen plots were located in recently burned marshes (0-1 years-since-burn or YSB); the remaining twenty-six plots were located in non-recently burned marshes ($\geq$2 YSB). Occupancy probability was higher at recently burned plots than non-recently burned plots at Mackay Island NWR (0.95 ± 0.06 vs. 0.69 ± 0.13) and at Back Bay NWR (0.73 ± 0.20 vs. 0.25 ± 0.12). The estimated plot abundance of King Rails was greater at Mackay Island NWR (1.47 ± 0.38) than at Back Bay NWR (0.66 ± 0.22). Although evidence suggested that King Rails responded positively to prescribed burns, I found no difference ($p>0.05$) in vegetation richness, canopy cover or horizontal cover between fire management categories. It is possible that King Rail response was mediated by other factors affecting habitat quality, such as food availability.

1.2 Introduction

King Rails (*Rallus elegans*) are secretive marsh birds that occupy freshwater, oligohaline and brackish marshes with robust, emergent vegetation and shallow water throughout their life cycle (Cooper 2008; Poole, Bevier, Marantz & Meanley 2005). From 1966 to 2009, North American populations have experienced significant range-wide declines (4.6%/year) due to the loss of suitable habitat, although the rate of decline for data collected after 1999 (2.8%/year) is not significant (Cooper 2008; Hunter, Golder, Melvin & Wheeler 2006; Sauer et al. 2011). In the Southeastern United States, many inland populations have declined, restricting King Rails mostly to coastal marshes (Cooper 2008; Hunter et al. 2006; Poole et al. 2005). Since 1986, an estimated 554,120 ha of freshwater emergent wetlands have been lost in the Southeast due to agricultural development, urbanization and salt intrusion (Dahl 2000; Dahl 2006; Hunter et al. 2006; Paxton 2006). Resulting from habitat loss, King Rail populations in the Southeast have declined 10.2%/year since 1980; and specifically in the Southeastern Coastal Plain, 3%/year since 1999 (Sauer et al. 2008; Sauer et al. 2011). These trends provide a starting point for estimating King Rail populations; however, they may not be accurate estimates, especially at smaller state or local scales, due to the lack of precision in the results (Sauer et al. 2011). In North Carolina and Virginia, King Rails are considered vulnerable according to their Natural Heritage Rank, and are listed as a Species of Conservation Concern on the states' Wildlife Action Plans (Cooper 2008; North Carolina Wildlife Resource Commission 2005; Virginia Department of Game and Inland Fisheries 2005).

Range-wide, little is known about the ecology of this species (Cooper 2008). Studies have only recently begun quantifying King Rail occurrence patterns and the habitat characteristics influencing them (Budd 2007; Darrah 2008; Pierluissi 2006). In 2006 the U.S. Fish and Wildlife Service (USFWS) initiated a project to step-down regional population and habitat objectives to management units (*e.g.*, wildlife refuges) in an effort to set in motion conservation practices to conserve the species at multiple scales (Drew, McKerrow & Earsom 2006). The pilot phase of this project focused on marsh habitats in Eastern North Carolina and Southeastern Virginia, with refuges and other management areas within the extent serving as the "local" scale to which regional objectives would be stepped down. Two of these focal areas were Mackay Island National Wildlife Refuge (NWR) in North Carolina and Back Bay NWR in Virginia. King Rails are a priority species of management concern at both refuges, are present year-round and are commonly detected at Mackay Island NWR, but are uncommonly detected at Back Bay NWR (USFWS 2008; USFWS 2010). Both refuges maintain King Rail marsh habitat through the use of prescribed burns, although fire management was not specifically implemented for King Rails. Fire is used to remove stands of dead *Phragmites australis* after herbicide spraying (USFWS 2010). Prescribed burning is also utilized in the refuges to maintain suitable marsh habitat for wildlife by limiting the growth of trees and shrubs and by removing other dead vegetation (Davison 1986; Nyman & Chabreck 1995; USFWS 2010). Uneven ground elevations at these refuges result in approximately 75% coverage by prescribed burns, leaving small patches of vegetation throughout the burn unit, particularly in areas with deeper water (J. B. Gallegos, USFWS, Back Bay NWR, pers. comm.). Fire effectively reduces the litter layer and increases the percent of bare ground, primary productivity, and the live to dead biomass ratio of burned plots (de Szalay & Resh 1997; Flores, Bounds & Ruby 2011; Hackney & de la Cruz 1981; Schmalzer, Hinkle & Mailander 1991). An understanding of King Rail response to fire as a management practice was of particular interest because although previous work suggested that fire adversely affected vegetation cover, and thus, use of marsh habitat by rails (Sikes 1984), more recent work suggested otherwise (Conway, Nadeau & Piest 2010). Yuma Clapper Rails (*Rallus longirostris yumanensis*) and Virginia Rails (*Rallus limicola*) responded positively to prescribed burn, while California Black Rails (*Laterallus jamaicensis coturniculus*), Soras (*Porzana carolina*) and Least Bitterns (*Ixobrychus exilis*) were not affected (Conway et al. 2010).

The dearth of information on rail ecology and the uncertainty surrounding the response of rails to prescribed burns in Southeastern United States provided an impetus for this work. Here I report estimates of site occupancy and abundance of King Rails in coastal Virginia and North Carolina based on surveys conducted in 2010. In addition, I evaluate the influence of prescribed burns on these parameters, and compare microhabitat characteristics of recently and non-recently burned marsh habitat. I discuss the conservation implication of these results for the Southeast region, including how they can be used to inform management decisions and how they address population and habitat goals outlined in the Conservation Action Plans for Back Bay NWR and Mackay Island NWR (USFWS 2008; USFWS 2010).

Study Area

This study was conducted in freshwater tidal, oligohaline and brackish marshes of the Back Bay region, specifically, Mackay Island NWR and Back Bay NWR (Figure 1.1). The refuges have changing water levels and salinities resulting from wind-driven tides (USFWS 2008); however, the salinity throughout most of the study area was less than 5 ppt. Mackay Island NWR lies on Knotts Island in Virginia Beach, VA and Currituck County, NC. Of the refuge's 3,326 ha, 1,932 ha are classified as freshwater tidal marshes (USFWS 2008). The Yarborough property, a private marsh hunt club, is collaboratively managed with Mackay Island NWR and was included in the analysis of Mackay Island NWR. Back Bay NWR encompasses 3,691 ha in Virginia Beach, VA (USFWS 2010). Back Bay NWR has 13 impoundments (457 ha) which are managed for resident and migratory bird populations (USFWS 2010). False Cape State

Park encompasses 1,179 ha in the City of Virginia Beach, VA, and has two impoundments that are collaboratively managed with Back Bay NWR (USFWS 2010; Virginia Department of Conservation and Recreation 2011). These two impoundments were included in the analysis of Back Bay NWR.

Marsh type differs between the two refuges. Mackay Island NWR consists primarily of natural marsh habitat with some impounded for wildlife management; whereas, Back Bay NWR has created marsh habitat. Both refuges are managed through the use of prescribed burns in three to five year cycles, although mowing may be used as a substitute for prescribed burns (USFWS 2008; USFWS 2010). Most burns are conducted in winter, but are occasionally as late as April. Burns are delayed because of wetness due to precipitation or wind tidal flooding (J. B. Gallegos, USFWS, Back Bay NWR, pers. comm.). Marshes with different fire histories were available at both refuges during the survey period (Figure 1.2).

Common freshwater emergent wetland vegetation present in the study area includes cattail (*Typha* spp.), cordgrass (*Spartina* spp.), bulrush (*Scirpus* sp.) and rosemallow (*Hibiscus* sp.) (Meanley 1969; Schafale & Weakley 1990). Previous ocean inlets along the Outer Banks have influenced the marsh vegetation, which is more characteristic of brackish marshes and include species such as black needle rush (*Juncus roemerianus*) and saltmeadow cordgrass (*Spartina patens*; Schafale & Weakley 1990; USFWS 2008). *J. roemerianus* tends to dominate stands that are not frequently burned (USFWS 2008). In addition, common reed (*Phragmites australis*) has also invaded the refuges (USFWS 2008; USFWS 2010).

1.3 Methods

From 27 April to 28 June 2010, observers surveyed 41 plots, each having a 200 m radius (Figure 1.3). Of these plots, 17 were located at Back Bay NWR, and 24 were located at Mackay Island NWR. Potential survey plots were mapped across the study area using a random-origin grid with points spaced 400 m apart. Point spacing ensured that individuals were not counted in multiple surveys (Conway 2008). Potential plots were characterized by patch size, distance to open water and fire management history. Observers selected among these plots based on two criteria: 1) accessibility ($\leq$ 500 m from road or boat access), which allowed three plots to be surveyed each day, and 2) equal representation of plot characteristics. At each refuge, observers surveyed plots from all available fire histories (Figure 1.4). I used ArcMAP 9.3.1 (ESRI 2009) to create shape files from refuge fire history data, and added survey plots to the maps to identify their burn histories. I defined two categorizes of fire management history: recently burned plots had been burned in the same or previous year (0-1 YSB), and non-recently burned plots had been burned two or more years prior ($\geq$2 YSB; Figure 1.5). This grouping yielded 15 plots in recently burned marsh and 26 in non-recently burned marsh, allowing for comparisons between fire categories (Table 1.1).

The call-broadcast surveys conducted from the center of each survey plot followed the North American Marsh Bird Monitoring Protocols (Conway 2008). Observers played a CD recording of marsh bird calls at a volume of 80-90 dB measured 1 m in front of the speakers (Conway 2008). The call-broadcast was ten minutes in length and consisted of five minutes of silence followed by five minutes of calls for five potentially breeding species, including Black Rail, Least Bittern, Virginia Rail, King Rail and Common Moorhen (*Gallinula chloropus*). For each species, the recording played 30 seconds of calls associated with breeding followed by 30 seconds of silence (Conway 2008). Observers recorded species detections throughout the survey period (Figure A.1). Each plot was surveyed three times during the breeding season with 10-12 d intervals (Rush, Soehren, Woodrey, Graydon & Cooper 2009). Since wind speed has been found to negatively affect detection probability, observers measured on-site wind speed using an anemometer and recorded data using a Beaufort scale (Conway 2008; Conway & Gibbs 2011). These data indicated that the average wind speed at the survey plots averaged 0.95 on the Beaufort scale or 2-5 km/h.

I used program PRESENCE, version 3.1 to estimate occupancy probability and abundance of King Rails in the study area (Hines 2006; MacKenzie et al. 2006; Royle & Nichols 2003). For these models, I created encounter histories for each plot by converting survey counts to detection-non-detection data (Table 1.2) and incorporated five survey plot characteristics as site covariates (Table 1.3). I created an *a priori* candidate set of 11 models to estimate occupancy (Ψ) and evaluate the influence of covariates (Table 1.4). To construct models, I first assessed whether detection probability was constant, time-specific over the survey season, dependent on fire history or dependent on location. Then, I added site covariates to the model structure with the best support (Franklin et al. 2004). I used the Royle/Nichols Abundance Induced Heterogeneity Model in PRESENCE to estimate the mean site abundance ($\hat{\lambda}$) of King Rails and included fire history and location as model covariates (Royle & Nichols 2003). The estimated number of King Rails in the surveyed habitat ($\hat{N}$) was calculated by multiplying $\hat{\lambda}$ by the number of sites surveyed. Density was then calculated by dividing $\hat{N}$ by the total surveyed area. These abundance estimates are specific to this study area and are not meant to be extrapolated to a larger setting.

I used Akaike's Information Criterion (AIC) to evaluate the support in the data for models in the candidate set and the strength of each covariate's effect on King Rail site occupancy (Burnham & Anderson 2002). Models with ΔAIC ≤ 2 were considered to have substantial support in the data. The influence of a covariate was deemed strong if the 95% CIs did not overlap zero.

Careful consideration of model assumptions was important for the interpretation of results. All occupancy models assumed that: 1) sites were "closed" to changes in occupancy during the study, 2) there were no false detections, and 3) detections across sites were independent (MacKenzie et al. 2002). Surveys were designed to help meet these assumptions. Surveys were conducted every 10-12 days (assumption 1). Observers were trained before conducting surveys (assumption 2). Plots were separated by at least 400 m (assumption 3). I also explicitly determined if models met assumptions by running a Pearson's goodness-of-fit test on the most supported model (MacKenzie & Bailey 2004). In addition to these assumptions, the Royle/Nichols model assumed that: 1) the number of animals at a particular site follows a defined spatial distribution for which lambda indicates the mean abundance across all sites, and 2) the probability of detecting animals at each site is related to the species' inherent detection probability, r, and the site abundance, N_i (Donovan & Hines 2007). The survey data were derived from a Poisson distribution (χ^2=5.644, p=0.06).

At each survey plot, observers recorded the following microhabitat characteristics: salinity (ppt) and water depth (cm) at the survey point and at cardinal points 30 m from the survey point (Conway 2008; Darrah 2008), vegetation richness within 1 m and percent cover of dominant wetland flora within 30 m of the survey point (Conway 2009), percent of canopy cover and percent of horizontal cover (Figure A.2). For canopy cover, observers measured the percent of canopy open using a concave spherical densiometer placed at the survey point (Lemmon 1956). Densiometers have not been previously utilized in marsh habitat; however, they provided a relative measure of closure based on consistent use. For horizontal cover, observers measured the number of squares obscured by vegetation on a 1.8 m x 0.3 m checkered density board at a distance of 1 m from the survey point. I made the density board from four sheets of white corrugated card board each measuring 0.3 m x 0.5 m and divided each sheet into twenty-four 0.08 m squares (Figure A.3). Observers attached the four sheets vertically to a PVC pole using velcro. This design gave the board more portability in the field. Each point had two measurements: the first in the North-South orientation, and the second in the East-West orientation. These measurements were then averaged. To facilitate comparison to previous studies (Darrah & Krementz 2009), I analyzed horizontal cover in three height increments: I considered below 0.5 m to be ground cover vegetation; below 1 m, short emergent vegetation; and above 1 m, tall emergent vegetation.

Microhabitat characteristics between recently and non-recently burned plots were compared using 2-sample t-tests (α=0.05) in JMP 8.0.1 (SAS Institute Inc. 2009). Microhabitat characteristics were also compared among all burn strata (*i.e.*, 0 YSB, 1 YSB, 2 YSB and $\geq$3 YSB), as well as between 0 YSB data and $\geq$1 YSB data, using non-parametric 1-sample Wilcoxon rank-sum tests in JMP 8.0.1 (SAS Institute Inc. 2009). I ran these additional tests to ensure that my habitat grouping by burn history, 0-1 YSB and $\geq$2 YSB, was not masking potential differences at a finer temporal resolution, that is, yearly intervals. All estimates are reported with standard error (± SE).

1.4 Results

A model featuring location and fire history as site covariates and detection probability dependent on location best explained occupancy of the study area by King Rails (AICw=0.60; Table 1.5). The estimated occupancy probability at Back Bay NWR for recently burned plots was 0.77 ± 0.20; and for non-recently burned plots, 0.28 ± 0.13. The estimated detection probability at Back Bay NWR was 0.50 ± 0.00. The estimated occupancy probability at Mackay Island NWR for recently burned plots was 0.95 ± 0.06; and for non-recently burned plots, 0.68 ± 0.13. The estimated detection probability at Mackay Island NWR was 0.76 ± 0.06. Location and fire history had strong influences on occupancy (*burn* $\hat{\beta}$=2.12 ± 1.16; *location* $\hat{\beta}$=1.70 ± 0.84). The goodness-of-fit test indicated that model assumptions were met (χ^2=1.45, p=0.95).

A Royle/Nichols model featuring location as a covariate best explained mean plot abundance of King Rails (AICw=0.88; Table 1.6). The estimated mean site abundance ($\hat{\lambda}$) for sites located at Back Bay NWR was 0.66 ± 0.22; the estimated inherent detection probability ($\hat{r}$) was 0.42 ± 0.11. An abundance estimate of population size ($\hat{N}$) across all Back Bay NWR plots was 11.18 (95%CI = 5.85 - 21.35). This corresponded to a density of 1 King Rail/16.67 ha of marsh habitat sampled in the refuge. The estimated mean site abundance ($\hat{\lambda}$) for plots at Mackay Island NWR was 1.47 ± 0.38; the estimated inherent detection probability ($\hat{r}$) was 0.62 ± 0.10. The estimated abundance for plots surveyed at Mackay Island NWR was 35.29 (95%CI = 21.18 - 58.80), corresponding to a density of 1 King Rail/8.33 ha.

There were no differences in vegetation richness (p=0.31), the percent of canopy open (p=0.99), horizontal cover by ground cover (p=0.31), horizontal cover by short vegetation (p=0.20), horizontal cover by tall vegetation (p=0.40), mean salinity (p=0.42) or mean water depth (p=0.64) between recently burned and non-recently burned plots (Table 1.7). There were no differences among 0 YSB, 1 YSB, 2 YSB and ≥3 YSB in vegetation richness (p=0.18), the percent of canopy open (p=0.94), horizontal cover by ground cover (p=0.56), horizontal cover by short vegetation (p=0.72), horizontal cover by tall vegetation (p=0.93), mean salinity (p=0.50) or mean water depth (p=0.97; Table 1.8). When 0 YSB microhabitat data were compared to ≥1 YSB, vegetation richness was greater in 0 YSB (p=0.04); however, there were no differences in the percent of canopy open (p=0.55), horizontal cover by ground cover vegetation (p=0.20), horizontal cover by short vegetation (p=0.46), horizontal cover by tall vegetation (p=0.74), mean salinity (p=0.17) or mean water depth (p=0.62; Table 1.9). Recently and non-recently burned plots representative of the study area are provided in Figure 1.6.

1.5 Discussion

King Rails occurred and were detected with higher probability in study plots at Mackay Island NWR than at Back Bay NWR. Likewise, their estimated abundance was greater at Mackay Island NWR than at Back Bay NWR. Regardless of location, King Rails responded positively to prescribed burns. There was poor support in the data for the influence of other covariates (*e.g.*, water depth, salinity and vegetation characteristics) on occupancy or abundance.

Occupancy rates reported here appear higher than in other studies that also followed standardized call-broadcast protocols and adjusted for detection probability. However, occupancy estimates may not be directly comparable due to environmental differences (*e.g.*, type of vegetation, wind speed), which affect the maximum distance that birds can be detected, and thus, the effective sampling area. Pierluissi (2006) estimated King Rail occupancy in Louisiana rice fields during the 2004 breeding season to be 0.35 ± 0.11 using data from 30 plots surveyed 5 times each, and during the 2005 breeding season to be 0.78 ± 0.82 using data from 60 plots surveyed 3 times each. Budd (2007) estimated King Rail occupancy in Arkansas during the 2005 breeding season to be 0.22 ± 0.07 using data from 69 plots surveyed up to 15 times each, and during the 2006 breeding season to be 0.06 ± 0.03 using data from 88 plots surveyed up to 9 times each. Darrah (2008) estimated King Rail occupancy in the Upper Mississippi Valley during the 2006 breeding season to be 0.11 ± 0.04 using data from 83 plots surveyed 7 to 9 times each, and during the 2007 breeding season to be 0.14 ± 0.04 using data from 114 plots surveyed 5 to 7 times each.

The higher occupancy rates recorded at Mackay Island and Back Bay NWRs were likely due to the predominance of freshwater and brackish emergent marshes in these refuges. King Rails occupy habitat with low average salinities, and while the study area had historical influxes of salt water due to previous ocean inlets, the salinity range did not exceed values known to support King Rail populations, nor did they reach levels preferred by Clapper Rails (Cooper 2008; USFWS 2008). Therefore, these occupancy and abundance estimates were likely not inflated by the presence of Clapper Rails. Differences between Mackay Island NWR and Back Bay NWR showed that occupancy varied even within this favorable context. Based on landscape level models (C. A. Drew & J. A. Collazo, NCSU, Dept. Biology, pers. comm.), marsh patch sizes, which were positively associated with King Rail occupancy, were greater at Mackay Island NWR than Back Bay NWR or other marshes in Eastern NC or Southeastern VA. Marsh type could also account for refuge differences. Mackay Island NWR survey plots consisted more of natural marsh; whereas, Back Bay NWR survey plots consisted of created impoundments. In addition, observers encountered muskrats and crayfish at Mackay Island NWR, species that have been anecdotally associated with King Rails (Cooper 2008; Meanley 1969; Poole et al. 2005). Therefore, the occupancy estimates in burned habitats, particularly those at Mackay

Island NWR, may be enhanced by the underlying presence of attributes increasing habitat quality.

Higher occupancy rates were accompanied with higher detection probabilities. Low on-site wind speed measurements suggested that detection probability was not biased by wind speed. There was also little evidence in the data that indicated an influence of burn history on detection. A remaining potential source of bias was density. Mackay Island NWR had a greater detection probability as well as a greater estimated abundance of King Rails, a finding consistent with previous studies (Conway & Gibbs 2011).

While this study supported a positive response to prescribed burns, previous research has suggested that King Rails may respond negatively, possibly because there was insufficient nesting cover after habitat is burned in early spring (Sikes 1984). The high occupancy rates reported herein and findings regarding reproductive activity (Chapter 2) were not consistent with this contention. King Rails did not appear to use survey plots with a mixture of recently and non-recently burned habitat more than survey plots completely contained within recently burned habitat. This suggests that King Rails did not require non-recently burned habitat in close proximity (*i.e.*, within the 200 m radius plot) to attain sufficient cover. Moreover, I did not find differences in microhabitat between recently and non-recently burned plots or differences in cover between 0 YSB plots and all other plots, indicating that sufficient cover was present after winter burns. Disparity in study conclusions may be due to differences in study design, as well as potential differences in other environmental variables that would affect a post-burn vegetation response (Gabrey, Afton & Wilson 1999; Mitchell, Gabrey, Marra & Erwin 2006). I was able to survey multiple recently burned plots; whereas, Sikes (1984) had a small sample size with only one recently burned plot. In addition, I included formal vegetation surveys to test for differences between fire categories. In this study, the lack of differences in cover may be explained by the dominance of *Spartina*, *Juncus* and *Typha* in the study area, which have been found to re-sprout readily after burns (Conway et al. 2010; Flores et al. 2011; Isacch, Holz, Ricci & Martinez 2004; Schmalzer et al. 1997). Darrah (2008) did not find a relationship between occupancy and vegetation height, although previous research suggested its importance for rails (Lor & Malecki 2006). While King Rails appear to require a minimum vegetation height for nesting, vegetation density rather than vegetation height is more indicative of suitable habitat during the breeding season, and stem density has been found to increase after burns (Flores et al. 2011; Pierluissi 2006; Reid 1989).

This research was designed to supplement a broader project aimed at stepping-down population and habitat objectives for King Rails in the Southeast (Drew et al. 2006; Hunter et al. 2006). Specifically, I wanted to inform decisions about habitat management actions by assessing King Rail responses to prescribed burns at the management unit level (*i.e.*, wildlife refuge). Current management practices did not adversely affect the occurrence and abundance of King Rails at Mackay Island NWR and Back Bay NWR. However, I recommend that data from other refuges and management units be assessed in a similar fashion before results are generalized and applied to address regional habitat objectives. Such efforts should adjust occupancy estimates for detection probability in order to draw stronger inferences about rail-habitat relationships and allow comparisons across multiple sites (MacKenzie et al. 2006). In addition, alternative hypotheses (*e.g.*, increased food availability) should be tested to explain the basis of the positive King Rail response to prescribed burns.

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Table 1.1: The number of survey plots at each refuge and in each fire history category.

Fire History	Back Bay NWR	Mackay Island NWR	**Total**
Recent Burn (0-1 YSB)	4	11	15
Non-recent Burn (≥2 YSB)	13	13	26
Total	17	24	41

Table 1.2: Encounter histories coded in PRESENCE in a detection-non-detection format to model single season occupancy.

Site ID	Survey 1	Survey 2	Survey 3
621378	0	0	0
622650	0	0	0
622651	0	0	0
622664	0	0	0
622668	0	0	0
626280	1	1	1
626281	1	1	1
626876	1	1	1
626877	1	1	1
626878	0	0	0
627464	1	0	0
628051	1	1	0
628053	0	0	0
629200	0	0	0
629201	0	0	0
629215	1	0	1
629788	1	1	0
629789	0	1	0
630345	1	0	0
630350	1	1	1
630914	1	1	1
630915	1	0	1
630957	1	0	1
631474	1	1	1
632075	0	0	0
632077	0	0	0
633140	1	1	0
633177	1	1	1
633178	1	1	0
633689	1	1	1
633690	0	1	1
633722	1	1	0
633724	0	1	1

Table 1.2: (continued)

Site ID	Survey 1	Survey 2	Survey 3
634265	0	0	0
634266	0	0	0
634779	0	0	0
635317	1	1	1
635319	0	1	1
999991	0	0	0
999992	0	0	0
999993	0	0	1

Table 1.3: Site covariates used to model occupancy in PRESENCE. The location covariate refers to survey plot placement at Mackay Island NWR.

Site ID	Burn	Edge	Depth	Salinity	Location
621378	0	0	1.000	6.600	0
622650	1	0	1.000	6.467	0
622651	0	1	0.667	10.615	0
622664	0	0	0.083	48.333	0
622668	0	0	1.538	16.200	0
626280	0	0	0.714	19.143	1
626281	0	0	0.385	21.867	1
626876	0	0	0.077	16.600	1
626877	0	0	0.571	9.133	1
626878	0	0	0.444	6.533	1
627464	0	0	0.200	15.286	1
628051	0	0	1.133	10.733	1
628053	0	0	0.750	15.800	1
629200	1	1	0.455	10.714	1
629201	0	0	1.286	4.643	1
629215	0	0	1.333	7.333	1
629788	1	1	1.700	9.286	1
629789	1	1	1.133	19.267	1
630345	1	1	0.818	14.308	1
630350	1	0	1.111	4.467	1
630914	1	0	1.000	11.133	1
630915	1	0	0.333	9.000	1
630957	0	0	1.600	6.786	0
631474	1	0	0.231	8.867	1
632075	0	0	2.000	4.933	0
632077	0	0	0.000	1.467	0
633140	1	0	0.600	8.133	1
633177	1	0	0.500	2.000	0
633178	1	0	1.100	5.600	0
633689	1	1	0.733	30.533	1
633690	1	1	1.214	4.333	1
633722	0	0	0.625	8.367	0
633724	1	1	0.875	4.600	0

Table 1.3: (continued)

Site ID	Burn	Edge	Depth	Salinity	Location
634265	0	0	5.600	3.818	0
634266	0	0	2.556	4.333	0
634779	0	0	0.429	15.667	1
635317	0	0	3.000	0.467	1
635319	0	0	0.429	13.467	1
999991	0	0	0.667	4.500	0
999992	0	0	0.111	7.867	0
999993	0	0	0.400	9.067	0

Table 1.4: Model notation and description for candidate models of King Rail site occupancy at Mackay Island NWR and Back Bay NWR.

Model Notation	Parameter Description
$\Psi(.)$	The probability of site occupancy is constant.
$\Psi(location)$	The probability of site occupancy depends on the location of the survey point, either Mackay Island NWR or Back Bay NWR. False Cape State Park survey points are categorized with Back Bay NWR, and the Yarborough property is categorized with Mackay Island NWR. This covariate encapsulates differences between refuges due to geographic location, as well as differences in attributes inherent to each refuge measured in this study, including marsh type (*i.e.*, natural or impounded) and patch size.
$\Psi(burn)$	The probability of site occupancy depends on the presence of recently burned habitat at the survey point.
$\Psi(depth)$	The probability of site occupancy depends on mean water depth at the survey point.
$\Psi(edge)$	The probability of site occupancy depends on the presence of both recently burned and non-recently burned habitat within the 200 m survey buffer.
$\Psi(salinity)$	The probability of site occupancy depends on the mean salinity at the survey point.
$\Psi(burn + location)$	The probability of site occupancy depends on the presence of recently burned habitat at the survey point and whether the survey point was located at Mackay Island NWR or Back Bay NWR. Points located at False Cape State Park are categorized with those located at Back Bay NWR.

Table 1.4: (continued)

Model Notation	Parameter Description
$\Psi(burn + edge)$	The probability of site occupancy depends on the presence of recently burned habitat at the survey point and the presence of non-recently burned habitat within the 200 m survey buffer.
$p(.)$	Detection probabilities are constant.
$p(t)$	Detection probabilities are survey-dependent.
$p(location)$	Detection probabilities are dependent on the location of the survey point, either Mackay Island NWR or Back Bay NWR. False Cape State Park survey points are categorized with Back Bay NWR, and the Yarborough property is categorized with Mackay Island NWR.
$p(burn)$	Detection probabilities are dependent on the presence of recently burned habitat at the survey point.

Table 1.5: A set of candidate models for a single season occupancy analysis ranked by their associated AIC values. Site covariates include the refuge in which the survey point was located, presence of recent burn at the survey point, the presence of a boundary between recent and non-recent burn within a 200 m survey buffer, mean salinity and mean water depth.

Model	AIC	ΔAIC	AICw	Model Likelihood	Parameters	-2LogLikelihood
$\Psi(burn + location), p(location)$	133.63	0.00	0.5950	1.0000	4	125.63
$\Psi(burn), p(location)$	135.96	2.33	0.1856	0.3119	3	129.96
$\Psi(location), p(location)$	136.71	3.08	0.1276	0.2144	3	130.71
$\Psi(burn + edge), p(.)$	139.19	5.56	0.0369	0.0620	4	131.19
$\Psi(.), p(location)$	140.44	6.81	0.0198	0.0175	2	136.44
$\Psi(depth), p(location)$	141.73	8.10	0.0104	0.0174	3	135.73
$\Psi(edge), p(location)$	141.74	8.11	0.0103	0.0173	3	135.74
$\Psi(salinity), p(location)$	142.43	8.80	0.0073	0.0123	3	136.43
$\Psi(.), p(.)$	142.85	9.22	0.0059	0.0100	2	138.85
$\Psi(.), p(burn)$	147.31	13.68	0.0006	0.0011	2	143.31
$\Psi(.), p(t)$	147.53	13.90	0.0006	0.0010	2	143.53

Table 1.6: Royle-Nichols Abundance Induced Heterogeneity Models for King Rail ranked by their associated AIC values. The refuge in which the point was located and the presence of recent burn at the survey point were used as site covariates.

Model	AIC	ΔAIC	AIC*w*	Model Likelihood	Parameters	-2LogLikelihood
Royle/Nichols with *location*	137.26	0.00	0.8783	1.0000	3	131.26
Royle/Nichols with *burn*	142.11	4.85	0.0777	0.0885	3	136.11
Royle/Nichols	143.25	5.99	0.0439	0.0500	2	139.25

Table 1.7: Comparisons of microhabitat variables measured within the period of known reproductive activity (21 May - 9 June) between 15 recently burned (0-1 YSB) and 26 non-recently burned (≥2 YSB) survey points (41 points total). Horizontal cover measurements consider the percents of vegetation cover at the ground cover (< 0.5 m), cover by short vegetation (< 1 m) and cover by tall vegetation (> 1 m). Comparisons were made using 2-sample t-tests. Estimates are reported with standard errors (± SE).

Microhabitat Variable	Recent Burn Mean	Non-recent Burn Mean	P-value
Vegetation Richness	6.33 ± 0.79	5.31 ± 0.46	p=0.31
Percent of Canopy Open	24.27 ± 9.12	22.88 ± 6.58	p=0.99
Horizontal Cover (< 0.5 m)	97.64 ± 2.36	94.07 ± 3.91	p=0.31
Horizontal Cover (< 1 m)	89.79 ± 5.25	81.97 ± 5.21	p=0.21
Horizontal Cover (> 1 m)	34.58 ± 9.25	37.66 ± 6.54	p=0.40
Salinity (ppt)	0.85 ± 0.10	1.06 ± 0.23	p=0.42
Water Depth (cm)	9.91 ± 1.85	11.14 ± 1.85	p=0.64

Table 1.8: Microhabitat comparisons of variables measured within the period of known reproductive activity (21 May - 9 June) among all burn strata: 0 YSB (n=7), 1 YSB (n=8), 2 YSB (n=5) and ≥3 YSB (n=21). Horizontal cover measurements consider the percents of vegetation cover at the ground cover (< 0.5 m), cover by short vegetation (< 1 m) and cover by tall vegetation (> 1 m). Comparisons were made using 1-sample Wilcoxon rank-sums tests. Estimates are reported with standard errors (± SE).

Microhabitat Variable	0 YSB Mean	1 YSB Mean	2 YSB Mean	3+ YSB Mean	P-value
Vegetation Richness	8.00 ± 1.31	4.88 ± 0.64	4.40 ± 1.12	5.52 ± 0.51	p=0.17
Percent of Canopy Open	33.58 ± 15.22	16.12 ± 10.86	24.44 ± 19.00	22.58 ± 7.17	p=0.94
Horizontal Cover (< 0.5 m)	100.00 ± 0.00	95.57 ± 4.43	92.08 ± 7.92	94.54 ± 4.54	p=0.56
Horizontal Cover (< 1 m)	90.33 ± 6.86	89.32 ± 8.25	77.29 ± 11.47	83.09 ± 5.95	p=0.72
Horizontal Cover (> 1 m)	39.14 ± 12.38	30.60 ± 14.18	25.00 ± 9.55	40.68 ± 7.71	p=0.93
Salinity (ppt)	1.04 ± 0.15	0.69 ± 0.12	1.23 ± 0.49	1.02 ± 0.27	p=0.50
Water Depth (cm)	10.80 ± 3.93	9.14 ± 1.06	9.40 ± 2.68	11.55 ± 2.21	p=0.97

Table 1.9: Comparisons of microhabitat variables measured within the period of known reproductive activity (21 May - 9 June) between 0 YSB habitat (n=7) and all other burn strata (n=34). Horizontal cover measurements consider the percents of vegetation cover at the ground cover (< 0.5 m), cover by short vegetation (< 1 m) and cover by tall vegetation (> 1 m). Comparisons were made using 1-sample Wilcoxon rank-sums tests. Estimates are reported with standard errors (± SE).

Microhabitat Variable	0 YSB Mean	1+ YSB Mean	P-value
Vegetation Richness	8.00 ± 1.31	5.21 ± 0.38	p=0.04
Percent of Canopy Open	33.58 ± 15.22	21.24 ± 5.58	p=0.55
Horizontal Cover (< 0.5 m)	100.00 ± 0.00	94.42 ± 3.14	p=0.20
Horizontal Cover (< 1 m)	90.33 ± 6.86	83.70 ± 4.41	p=0.46
Horizontal Cover (> 1 m)	39.14 ± 12.38	36.00 ± 5.92	p=0.74
Salinity (ppt)	1.04 ± 0.15	0.97 ± 0.18	p=0.17
Water Depth (cm)	10.80 ± 3.93	10.67 ± 1.43	p=0.62

Figure 1.1: The study region includes marsh habitat located in Southeastern Virginia and Northeastern North Carolina at Back Bay National Wildlife Refuge, False Cape State Park and Mackay Island National Wildlife Refuge.

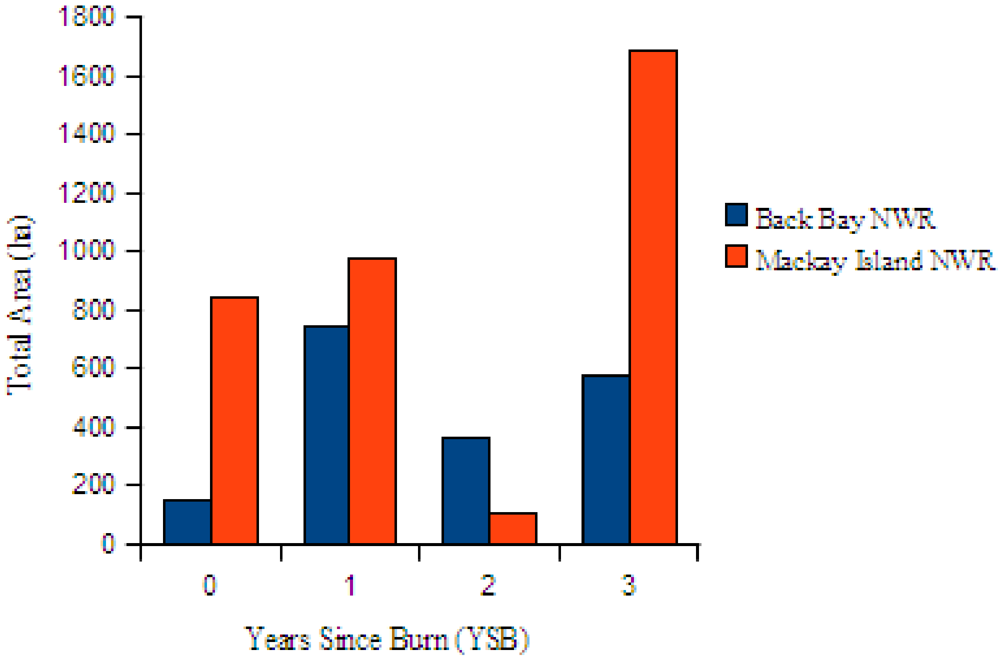


Figure 1.2: Area (ha) of marsh habitat present during the survey period grouped by fire history. The 3 YSB group includes all plots that had not been burned within 3 years of the survey period, including plots that are not managed with prescribed burns.

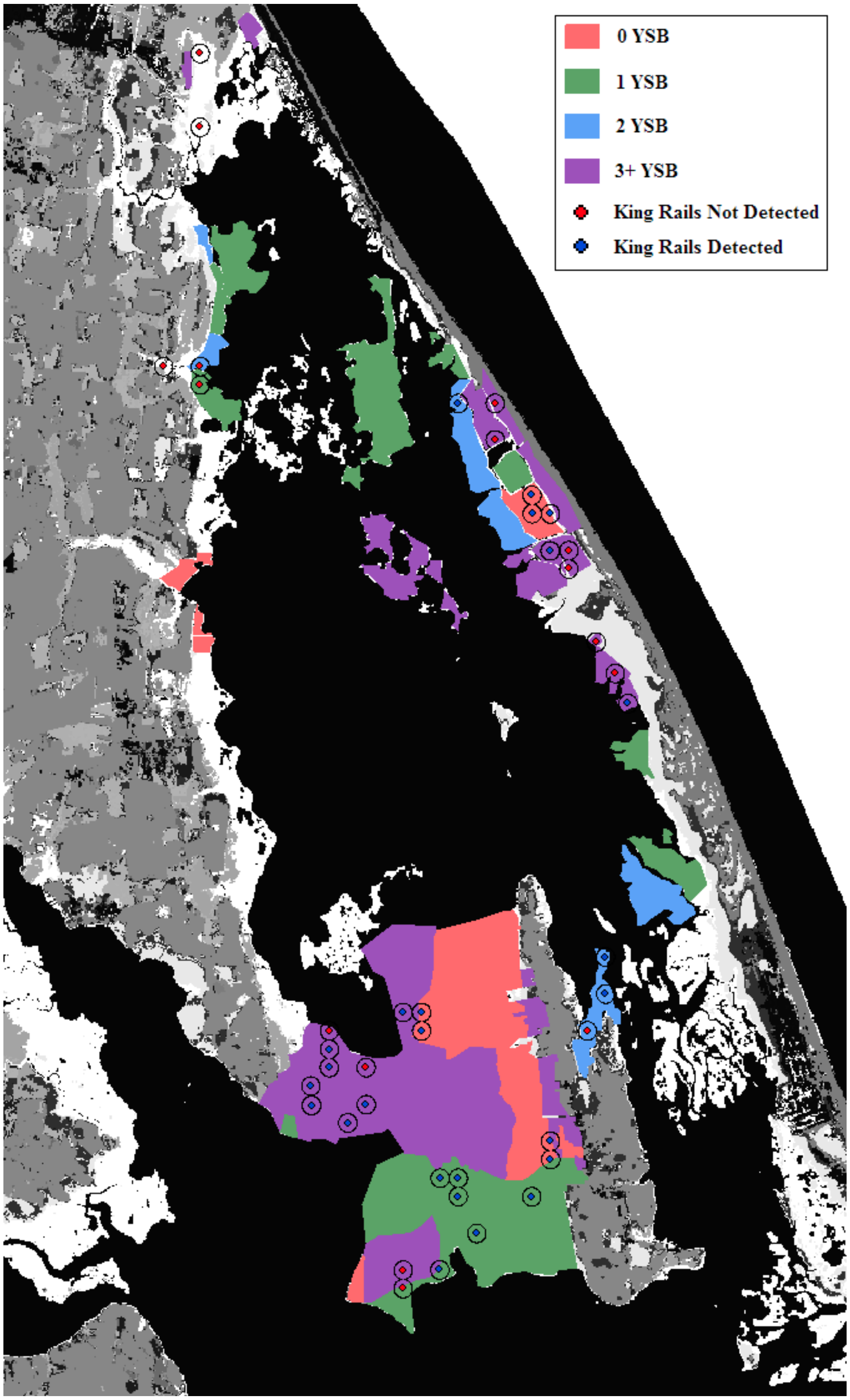


Figure 1.3: Call-broadcast survey site locations and detections at Mackay Island NWR, Back Bay NWR and False Cape State Park during the 2010 breeding season. The study area is colored according to fire management history, and sites are colored by detections. Sites were selected from a systematic grid overlaying marsh habitat such that points were spaced 400 m apart. Sites are shown with 200 m buffers.

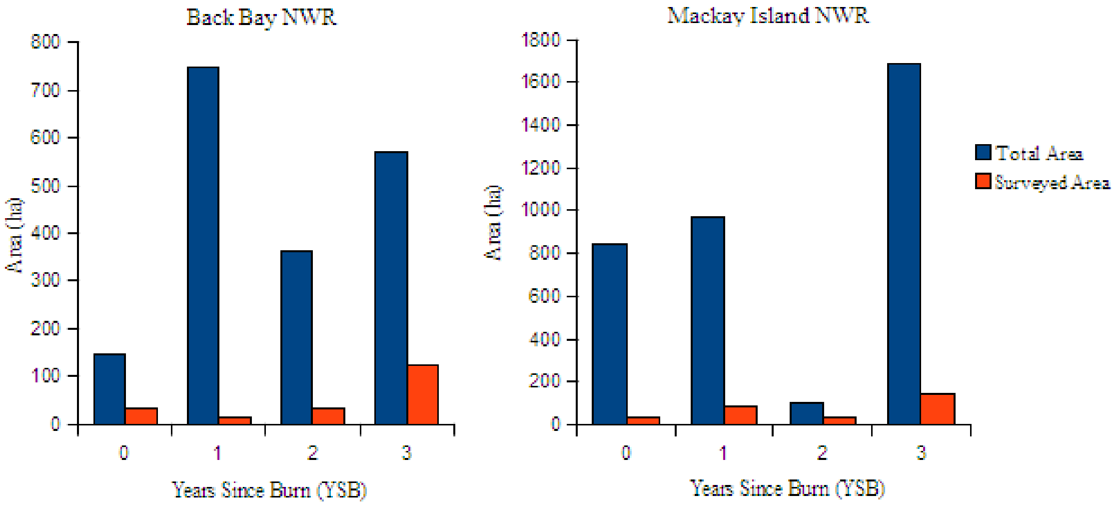


Figure 1.4: Estimated total area (ha) and surveyed area at each refuge grouped by fire history. The 3 YSB group includes all plots that had not been burned within 3 years of the survey period, including plots that are not managed with prescribed burns.

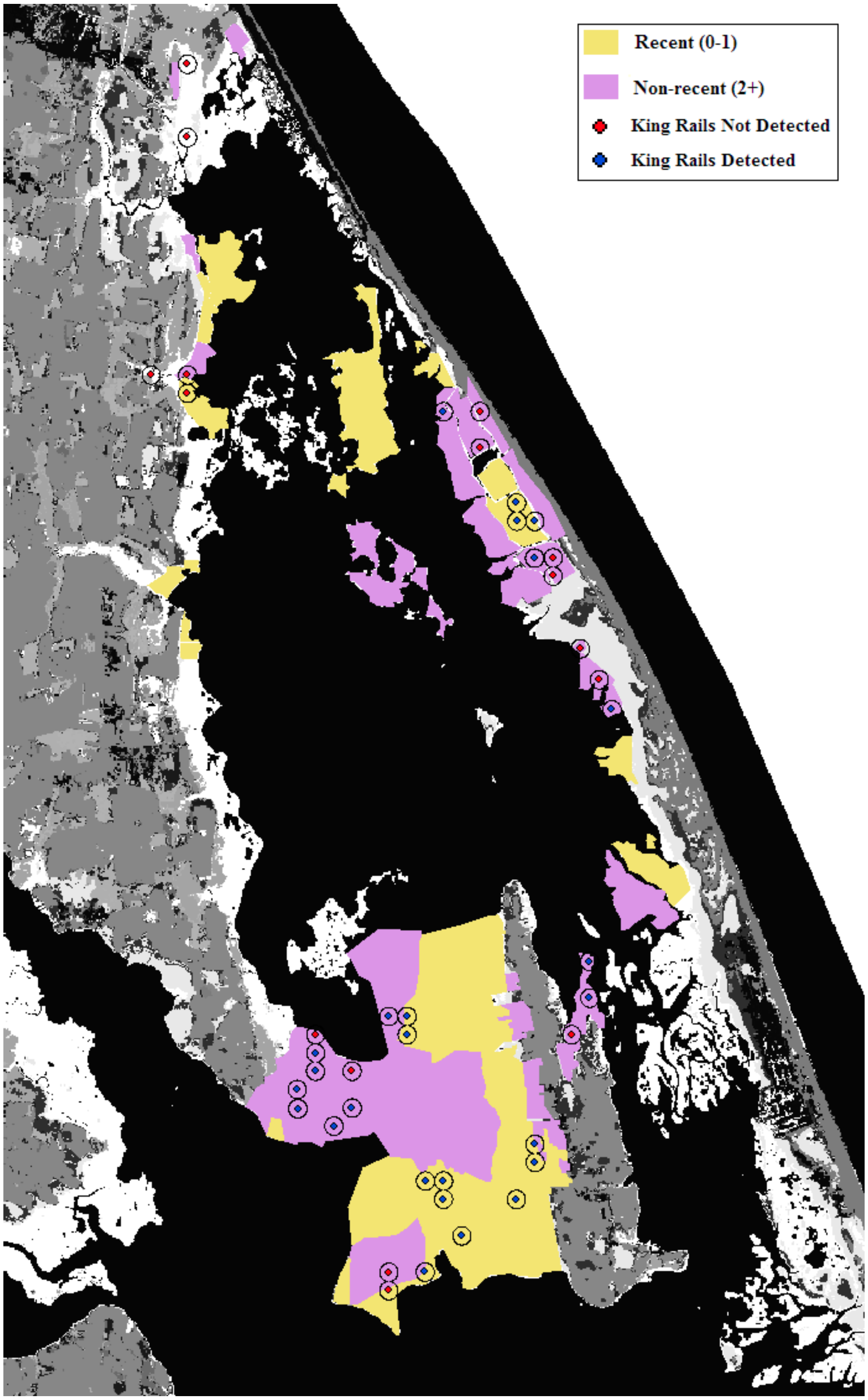


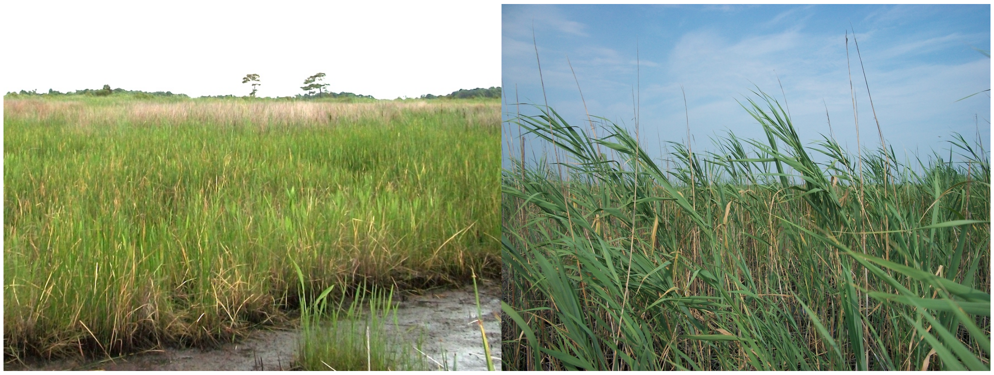
Figure 1.5: Call-broadcast survey site locations and detections at Mackay Island NWR, Back Bay NWR and False Cape State Park during the 2010 breeding season. The study area is colored by recent (0-1 YSB) and non-recent (≥ 2 YSB) burns, and sites are colored by detections. Sites were selected from a systematic grid overlaying marsh habitat such that points were spaced 400 m apart. Sites are shown with 200 m buffers.

(a) 0 YSB, Survey 1

(b) 3 YSB, Survey 1

(c) 0 YSB, Survey 2

(d) 3 YSB, Survey 2



(e) 0 YSB, Survey 3

(f) 3 YSB, Survey 3

Figure 1.6: Recently and non-recently burned habitats representative of the study area during each of the three surveys.

Chapter 2

Linking occupancy, reproductive activity and nest success of King Rails in managed coastal marshes of North Carolina and Virginia

2.1 Abstract

King Rails (*Rallus elegans*) are declining marsh birds that primarily occupy freshwater marshes with emergent vegetation and shallow water. A greater understanding of the King Rail's breeding ecology is required to curb declining trends. My objectives were to: 1) estimate the probability of detecting reproductive activity, 2) estimate nest success, and 3) determine habitat preference and site characteristics of nesting King Rails at Back Bay and Mackay Island National Wildlife Refuges (NWR). I modeled the probability of detecting reproductive activity as a function of fire management history. During 2009 and 2010, 14 nests were detected in recently burned marshes (0-1 YSB), and 2, in non-recently burned marshes ($\geq$2 YSB). The probability of detecting reproductive activity in recently burned marshes was 0.75 ± 0.19 at Mackay Island NWR and 0.25 ± 0.21 at Back Bay NWR. These estimates were higher than in non-recently burned marshes at the same locations (Mackay Island NWR = 0.22 ± 0.17; Back Bay NWR = 0.03 ± 0.04). Daily nest survival probability (0.97 ± 0.02) was negatively influenced by the time nests were left unattended. Period survival for the incubation stage was 0.58. Evidence suggested that King Rails exhibited higher nesting activity in recently burned marshes, although microhabitat characteristics were not strong determinants of that response. Vegetation richness and cover did not differ between nest sites and random locations ($p > 0.05$).

Linkages between occupancy and reproductive activity (egg stage) in the context of prescribed burns were established. However, a full assessment of the demographic benefits of recently burned marshes to King Rails requires that brood survival be quantified.

2.2 Introduction

King Rails (*Rallus elegans*) are declining secretive marsh birds that occupy freshwater, oligohaline and brackish marshes with robust, emergent vegetation and shallow water throughout their life cycle (Cooper 2008; Poole, Bevier, Marantz & Meanley 2005). In the Southeastern United States, population numbers have declined at an annual rate of 10.2% since 1980 (Sauer, Hines & Fallon 2008). Habitat loss and degradation have restricted populations mostly to coastal marshes (Cooper 2008; Hunter, Golder, Melvin & Wheeler 2006; Meanley 1969, Poole et al. 2005), and it is believed that this shift has contributed to population declines in the region. Southeastern Coastal Plain populations show declines of 3%/year (Sauer et al. 2011). Conversion of freshwater emergent wetlands in the Southeast has been substantial, amounting to an estimated 554,120 ha since 1986 (Dahl 2000; Dahl 2006; Hunter et al. 2006). Salt intrusion also threatens the integrity and quality of coastal freshwater marshes (Paxton 2006).

Concerns about the species' status prompted the U.S. Fish and Wildlife Service (USFWS) to support research aimed at augmenting our knowledge about their ecology and response to habitat management practices to formulate strategies to curb population declines (Drew, McKerrow & Earsom 2006). This work has focused on marsh habitats in Eastern NC and Southeastern VA, specifically, in Mackay Island and Back Bay National Wildlife Refuges (NWR). Of great interest to this initiative was the King Rail's reproductive ecology and their response to prescribed burns. The aforementioned refuges manage marsh habitat through the use of prescribed burns during the fall, winter and sometimes early spring. Fire is primarily used to remove stands of dead *Phragmites australis* after herbicide spraying (USFWS 2010). Dense, monotypic stands of *P. australis* are not suitable habitat for breeding waterbirds (Benoit & Askins 1999). Prescribed burning is also utilized in the refuges to maintain suitable marsh habitat for wildlife by limiting the growth of trees and shrubs and by removing the litter layer (Davison 1986; Nyman & Chabreck 1995; USFWS 2010).

Little is known about the breeding ecology of King Rails, and much less about how breeding rails respond to prescribed burns (Cooper 2008). King Rails nest primarily in May and June, although nesting may start in February or March and continue through August in areas with longer warm seasons, such as Florida or Louisiana (Poole et al. 2005). They construct concealed nests in fairly uniform stands of vegetation (Meanley 1969). King Rails lay clutches of 10-12 eggs, laying a single egg daily. Egg laying is followed by 21 days of incubation by both parents (Meanley 1969; Poole et al. 2005). Semiprecocial chicks usually hatch within a 48-hour interval and can leave the nest the same day they hatch (Cooper 2006; Meanley 1969; Poole et al. 2005). Evidence is equivocal with regards to how prescribed burns might influence the reproductive performance of rails. For example, some studies reported that reproduction was adversely affected due to insufficient time for vegetation to recover after winter burns (Sikes 1984). In contrast, Conway, Nadeau & Piest (2010) found an increase in some rail species following winter and early spring burns.

In this study, I estimate nest survival of King Rails in coastal Virginia and North Carolina marsh habitats. I also ask whether the probability of detecting reproductive activity was linked to the probability of occupancy at a sampling unit, and whether this probability was influenced by fire management history. Finally, I determine whether rails used marsh habitat randomly with respect to fire history, and compare vegetation characteristics at two levels: 1) between nest locations and random plots, and 2) between nest locations and random plots within recently burned habitat. I discuss how my findings expand knowledge about the species' reproductive ecology and its conservation implications for Virginia and North Carolina, and elsewhere in the Southeastern United States.

2.3 Study Area

This study was conducted in freshwater tidal, oligohaline and brackish marshes of the Back Bay region, specifically, Mackay Island NWR and Back Bay NWR (Figure 2.1). The refuges have changing water levels and salinities resulting from wind-driven tides (USFWS 2008); however, the salinity throughout most of the study area was less than 5 ppt. Mackay Island NWR lies on Knotts Island in Virginia Beach, VA and Currituck County, NC. Of the refuge's 3,326 ha, 1,932 ha are classified as freshwater tidal marshes (USFWS 2008). The Yarborough property, a private marsh hunt club, is collaboratively managed with Mackay Island NWR and was included in the analysis of Mackay Island NWR. Back Bay NWR encompasses 3,691 ha in Virginia Beach, VA (USFWS 2010). Back Bay NWR has 13 impoundments (457 ha) which are managed for resident and migratory bird populations (USFWS 2010). False Cape State Park encompasses 1,179 ha in the City of Virginia Beach, VA, and has two impoundments that are collaboratively managed with Back Bay NWR (USFWS 2010; Virginia Department of Conservation and Recreation 2011). These two impoundments were included in the analysis of Back Bay NWR.

Marsh type differs between the two refuges. Mackay Island NWR consists primarily of natural marsh habitat with some impounded for wildlife management; whereas, Back Bay NWR has created marsh habitat. Both refuges are managed through the use of prescribed burns in three to five year cycles, although mowing may be used as a substitute for prescribed burns (USFWS 2008; USFWS 2010).Most burns are conducted in winter, but are occasionally as late as April. Burns are delayed because of wetness due to precipitation or wind tidal flooding (J. B. Gallegos, USFWS, Back Bay NWR, pers. comm.).

Common freshwater emergent wetland vegetation present in the study area includes cattail (*Typha* spp.), cordgrass (*Spartina* spp.), bulrush (*Scirpus* sp.) and rosemallow (*Hibiscus* sp.) (Meanley 1969; Schafale & Weakley 1990). Previous ocean inlets along the Outer Banks have influenced the marsh vegetation, which is more characteristic of brackish marshes and include species such as black needle rush (*Juncus roemerianus*) and saltmeadow cordgrass (*Spartina patens*; Schafale & Weakley 1990; USFWS 2008). *J. roemerianus* tends to dominate stands that are not frequently burned (USFWS 2008). In addition, common reed (*Phragmites australis*) has also invaded the refuges (USFWS 2008; USFWS 2010).

2.4 Methods

Occupancy and Reproductive Activity

From 27 April to 28 June 2010, observers surveyed 41 plots, each having a 200 m radius (Figure 2.2). Of these plots, 17 were located at Back Bay NWR, and 24 were located at Mackay Island NWR. Potential survey plots were mapped across the study area using a random-origin grid with points spaced 400 m apart. Point spacing ensured that individuals were not counted in multiple surveys (Conway 2008). Potential plots were characterized by patch size, distance to open water and fire management history. Observers selected among these plots based on two criteria: 1) accessibility ($\leq$ 500 m from road or boat access), which allowed three plots to be surveyed each day, and 2) equal representation of plot characteristics. I used ArcMAP 9.3.1 (ESRI 2009) to create shape files from refuge fire history data, and added survey plots to the maps to identify their burn histories. I defined two categorizes of fire management history: recently burned plots had been burned in the same or previous year (0-1 YSB), and non-recently burned plots had been burned two or more years prior ($\geq$2 YSB; Figure 2.3). This grouping yielded 15 plots in recently burned marsh and 26 in non-recently burned marsh, allowing for comparisons between fire categories.

The call-broadcast surveys conducted from the center of each survey plot followed the North American Marsh Bird Monitoring Protocols (Conway 2008). Observers played a CD recording of marsh bird calls at a volume of 80-90 dB measured 1 m in front of the speakers (Conway 2008). The call-broadcast was ten minutes in length and consisted of five minutes of silence followed by five minutes of calls for five potentially breeding species, including Black Rail, Least Bittern, Virginia Rail, King Rail and Common Moorhen (*Gallinula chloropus*). For each species, the recording played 30 seconds of calls associated with breeding followed by 30 seconds of silence (Conway 2008). Observers recorded species detections throughout the survey period (Figure A.1). Each plot was surveyed three times during the breeding season with 10-12 d intervals (Rush, Soehren, Woodrey, Graydon & Cooper 2009). Since wind speed has been found to negatively affect detection probability, observers measured on-site wind speed using an anemometer and recorded data using a Beaufort scale (Conway 2008; Conway & Gibbs 2011). These data indicated that the average wind speed at the survey plots averaged 0.95 on the Beaufort scale or 2-5 km/h. Upon completion of call-broadcast surveys, observers searched for nests. Searches were completed on every occasion regardless of previous knowledge of a nest or detection during the call-broadcast. Twenty-nine plots were searched from 30 March to 13 May 2009. Forty-one plots were searched from 27 April to 28 June 2010. Observers searched marsh habitat haphazardly; the terrain did not facilitate searching in linear transects. To ensure that plots were searched as thoroughly as possible, each observer documented search paths and times using a GPS receiver. Search effort for each site was standardized to one hour. The extent of search tracks was identified with ArcMAP 9.3.1 (ESRI 2009). Tracks showed that non-recently burned plots were searched as thoroughly as recently burned plots (Figure 2.4).

I used single season, multi-state models in program PRESENCE, version 3.1 to estimate the probability that a plot was occupied regardless of reproductive activity (Ψ^1) and the probability of detecting an active King Rail nest in an occupied plot (Ψ^2) during the 2010 breeding season (Hines 2006; MacKenzie et al. 2006; Nichols, Hines, MacKenzie, Seamans & Gutierrez 2007). For these models, I converted the survey and nest search data to encounter histories in a detection-non-detection format (Table 2.1) and incorporated five survey plot characteristics as site covariates (Table 2.2). In the multi-state framework, reproductive activity only has to be detected once per plot for proper model inference; that is, the sampling unit changes from a non-breeding state to a breeding state (Nichols et al. 2007). However, because a rail nest could be active over two consecutive survey occasions, I coded the data differently to avoid spurious estimates of Ψ^1 and Ψ^2. I created two codes for each sampling occasion, such that the encounter history based on three sampling occasions had six columns instead of the expected three columns (Table 2.1). Columns one, three and five corresponded to the call-broadcast survey results, and were coded as (1) if at least one rail was detected or (0) if no rails were detected. Columns two, four and six corresponded to the nest search results, and were coded as (2) if a nest was detected or (0) if no nest was detected. The detection probabilities $p^1(1)$, $p^1(3)$ and $p^1(5)$ corresponded to the probability of detecting a rail during the call-broadcast surveys at non-breeding sites. The detection probabilities $p^2(1)$, $p^2(3)$ and $p^2(5)$ corresponded to the probability of detecting a rail during the call-broadcast surveys at breeding sites. The detection probabilities $p^2(2)$, $p^2(4)$ and $p^2(6)$ corresponded to the probability of detecting a nest at breeding sites. The values for $p^1(2)$, $p^1(4)$ and $p^1(6)$ did not provide any information and were fixed to zero. This code also generated extra parameters that needed to be distinguished, which were also fixed in some cases to obtain appropriate parameter estimates. The parameter delta^1 (δ^1; the probability of correctly classifying the state of a plot based on call-broadcast surveys) was set equal to zero as no claim about reproductive activity was made from these data. Delta^2 (δ^2; the probability of correctly classifying the state of a plot based on nest searches) was set to equal one, because finding a nest was definitive evidence of reproduction (Donovan & Hines 2007; Nichols et al. 2007). Finally, I added the sampling covariate (*nest*) to adjust the probability of detecting a nest (*i.e.*, $p^2(2)$, $p^2(4)$, $p^2(6)$) for the presence of active nests on consecutive sampling occasions.

I created an *a priori* candidate set of 11 models to estimate occupancy (Ψ^1) and reproductive activity, given occupancy (Ψ^2), and evaluated the influence of the covariates (Table 2.4). To construct models, I first assessed whether detection probability was constant, time-specific over the survey season, or dependent on fire history or location. I added site covariates to the model structure with the best support (Franklin et al. 2004). I used Akaike's Information Criterion (AIC) to evaluate the support in the data for models in the candidate set and the strength of each covariate's effect (Burnham & Anderson 2002). Models with $\Delta\text{AIC} \leq 2$ were considered to have substantial support in the data. The influence of a covariate was deemed strong if the 95% CIs did not overlap zero. I also reported the unconditional probability of reproduction, that is, the probability that an active nest was present at a site. This was calculated as the product of the probability of site occupancy (Ψ^1) and the probability of reproduction conditioned on site occupancy (Ψ^2) using the parameter estimates from the model with the most support (Nichols et al. 2007).

Careful consideration of assumptions was important for the interpretation of results. Multi-state occupancy models assumed that: 1) sites were "closed" to changes in occupancy, 2) there were multiple site visits, 3) there was no false detection of evident reproduction, and (4) detections were independent across plots (MacKenzie et al. 2002; Nichols et al. 2007). Violation of the first assumption was minimized by conducting surveys as close as possible, in this study, every 10-12 days. Assumptions 2-4 were met, because each plot was surveyed and searched three times, nest detections provided definitive evidence of reproduction, and points were separated by 400 m (Conway 2008).

Habitat Selection

During the 2010 season, observers recorded the following microhabitat characteristics at each call-broadcast point and nest location: salinity (ppt) and water depth (cm) at the survey point and at cardinal points 30 m from the survey point (Conway 2008; Darrah 2008), vegetation richness within 1 m and percent cover of dominant wetland flora within a 30 m radius of the survey point (Conway 2009), percent of canopy cover and percent of horizontal cover (Figure A.2). For canopy cover, observers measured the percent of canopy open using a concave spherical densiometer placed at the survey point (Lemmon 1956). Densiometers have not been previously utilized in marsh habitat; however, they provided a relative measure of closure based on consistent use. For horizontal cover, observers measured the number of squares obscured by vegetation on a 1.8 m x 0.3 m checkered density board at a distance of 1 m from the survey point. I made the density board from four sheets of white corrugated card board each measuring 0.3 m x 0.5 m and divided each sheet into twenty-four 0.08 m squares (Figure A.3). Observers attached the four sheets vertically to a PVC pole using velcro. This design gave the board more portability in the field. Each point had two measurements: the first in the North-South orientation, and the second in the East-West orientation. These measurements were then averaged. To facilitate comparison to previous studies (Darrah & Krementz 2009), I analyzed horizontal cover in three height increments: I considered below 0.5 m to be ground cover vegetation; below 1 m, short emergent vegetation; and above 1 m, tall emergent vegetation. I compared microhabitat characteristics between points where a nest was found (n=9) and random points where no nest was found (n=41) using 2-sample t-tests (α=0.05) in JMP 8.0.1 (SAS Institute Inc. 2009). Random points were comprised of call-broadcast survey points.

To assess preference of nest locations relative to the availability of recently burned and non-recently burned habitats, I implemented randomization tests (Manly 2006) using Java. This distribution-free approach was adequate for small sample sizes (Manly 2006; Legendre & Legendre 1998), where chi-square goodness-of-fit tests lacked power (Wright 1992). In order for the randomization tests to be effective, King Rails must have had access to recently and non-recently burned habitats, and both habitat types had to be searched (Byers & Steinhorst 1984). The input required the number of nests found in a given burn stratum and the proportion of available habitat for each stratum. I used the area within the survey plots to develop these available proportions. During each simulation, the program randomized n nests, where n was the number of nests observed during the breeding season. The program generated n random numbers between 0 and 1. Each randomly generated number was assigned to the burn stratum whose availability interval category contained the random number (categories added up to 1.00). Intervals were defined as the proportion of available habitat within a given burn history stratum. Thus, each stratum received a simulated number of observations that is random and allocated based on its proportion of availability. This process was repeated 1,000,000 times, generating a total of 1,000,000 simulated breeding seasons of n nests each. For each burn stratum, the program calculated a p-value, the percentage of simulations in which the simulated number of nests was greater than the observed number of nests (Manly 2006). P-values were interpreted as the probability of observing a nest in a particular burn stratum under the null hypothesis of no preference. The p-values less than $\alpha = 0.05$, Bonferroni-corrected for multiple comparisons (*i.e.*, α/total burn strata), indicated nesting preference of the respective burn stratum.

Nest Surveillance and Success

Observers set up continuous video monitoring systems at nests to record for the duration of nest activity in order to track parental behavior and determine nest fate (Appendix B). Daily nest visits were required to check the system status, download data and trim vegetation around nests if line of sight from the video camera was inhibited. I watched video continuously on 8x speed and recorded instances of fixing vegetation, rotating eggs and unattended nests, as well as when two parents were present at the nest, when a predator was present at the nest, egg laying and hatching. I considered nests that hatched at least one egg to be successful and noted if any abandoned eggs were present at successful nests. I tested the effect of trimming vegetation on the duration of fixing vegetation during the following day. For the 11 nests that were monitored during the incubation period, vegetation was trimmed on 21 days; however, only 13 days of trimming were used in the analysis. Some days when vegetation was trimmed could not be included in the analysis due to monitoring system failure.

I also compiled full days of data among all nests for the beginning of incubation (*i.e.*, days 4, 5, and 6), the middle of incubation (*i.e.*, days 10, 11, 12, and 13) and the end of incubation (*i.e.*, days 16, 17, 18, and 19) and tested for differences in mean daily durations that nests were left unattended and that parents spent fixing vegetation (*i.e.*, nest maintenance) to determine if these behaviors had a seasonal component. Results indicated that neither the duration that nests were left unattended nor the duration spent fixing vegetation differed among throughout the incubation period (p=0.86 and p=0.17, respectively). Therefore, single mean daily duration estimates of parental absence and nest maintenance at each nest were calculated from all full days of data and used as covariates in nest survival models for the incubation period. The daily duration that nests were unattended ranged from 280 s to 3,750 s. The daily duration that parents invested on nest maintenance ranged from 33 s to 2,200 s (Table 2.5).

I estimated daily nest survival (DSR) and period survival rates (PSR) for nests monitored in 2009 and 2010 using program MARK (Dinsmore, White & Knopf 2002; White & Burnham 1999). I used 57 days for the length of the breeding season and assigned the dates of nest discovery and nest visits a day within the breeding season (1-57). I created a candidate set of 8 models to estimate nest survival for two data sets: 1) exposure data for the entire egg stage, 31 days, and 2) exposure data during the only the incubation stage, 21 days. Egg stage models allowed for the inclusion of nests that failed during egg laying. However, video data during egg laying were too few to be included in the behavioral covariates; thus, the effects of unattended nests and nest maintenance could only be tested in the incubation stage models. The model set also included constant and year-specific terms, as well as terms assessing evidence for seasonal patterns in daily survival (*i.e.*, linear and quadratic terms; Table 2.6). I could not model nest survival as a function of fire management history, because too few nests occurred in non-recently burned marsh.

I used Akaike's Information Criterion corrected for small samples (AICc) to evaluate the support in the data for models in the candidate set and the strength of each covariate's effect on King Rail nest survival (Burnham & Anderson 2002). When considering the egg stage, more than one model had substantial support (ΔAICc ≤ 2); thus, the estimated nest survival probabilities were averaged using AIC weights (Burnham & Anderson 2002). Non-interactive model averaging was available in program MARK (White & Burnham 1999), which produced an average daily survival rate ($\widehat{D\bar{S}R}$) for each day in the defined breeding season, for a total of 57 $\widehat{D\bar{S}R}$ values. I multiplied 31 $\widehat{D\bar{S}R}$ values beginning with the average estimated nest initiation day to obtain the model averaged PSR. I also multiplied the lower and upper 95% CIs for the same 31 $\widehat{D\bar{S}R}$ values to obtain the model averaged 95% CIs for PSR. Nest survival model assumptions included: 1) homogeneity of daily nest survival rates, 2) independent nest fates, 3) recorded nest visits, 4) no influence of nest visits on survival and nest fate, and 5) correct determination of nest fates and age of nests at discovery (Dinsmore et al. 2002). I believe that all assumptions were met. In particular, no evidence suggested that remote video monitoring increased nest predation rates, a finding also reported by Richardson, Gardali & Jenkins (2009).

2.5 Results

Occupancy and Reproductive Activity

The model that included *location* and *burn* as covariates best explained evidence for reproductive activity given occupancy (AICw = 0.92; Table 2.7). The influence of these covariates on occupancy and reproductive activity in occupied patches was strong (*burn* $\beta = 2.35 \pm 0.91$; *location* $\beta = 2.22 \pm 0.80$). The probability of detecting a rail during a call-broadcast survey for a plot occupied by non-breeders (*e.g.*, $p^1(1)$) was 0.77 ± 0.08. The probability of detecting a rail during a call-broadcast survey for a plot occupied by breeders (*e.g.*, $p^2(1)$) was 0.69 ± 0.11. The probability of detecting a nest given that a nest was present (*e.g.*, $p^2(2)$) was 0.24 ± 0.11.

The estimated occupancy probability in recently burned plots ($\hat{\Psi}^1$) at Mackay Island NWR was 0.96 ± 0.04, and the probability that active nests occurred in occupied plots ($\hat{\Psi}^2$) was 0.75 ± 0.19. The estimated unconditional probability that a site was occupied by an active nest was 0.72. For non-recently burned plots, $\hat{\Psi}^1$ was 0.71 ± 0.12, $\hat{\Psi}^2$ was 0.22 ± 0.17, and the estimated unconditional probability that a site was occupied by an active nest was 0.16. Estimated occupancy in recently burned plots ($\hat{\Psi}^1$) at Back Bay NWR was 0.73 ± 0.17, and the probability that active nests occurred in occupied plots ($\hat{\Psi}^2$) was 0.25 ± 0.21. The unconditional probability that a site was occupied by an active nest was 0.18. For non-recently burned plots, $\hat{\Psi}^1$ was 0.21 ± 0.10, $\hat{\Psi}^2$ was 0.03 ± 0.04, and the unconditional probability that a site was occupied by an active nest was 0.01.

Habitat Selection

In 2010, 167.49 ha (34.8%) of habitat searched was categorized as recent burn, and 313.17 ha (65.2%) of habitat searched was non-recent burn (Table 2.8). King Rails selected recently burned habitat in greater proportion than its availability ($p < 0.001$). Random points had a greater percent of horizontal cover by tall vegetation than nest locations ($p=0.03$); however, there were no differences in vegetation richness ($p=0.86$), the percent of canopy open ($p=0.54$), percent of horizontal cover by ground level vegetation ($p=0.09$) and percent of horizontal cover by short vegetation ($p=0.19$; Table 2.9). Contrasts between only random points and nest locations in recently burned habitat ($n=8$ and $n=15$, respectively) yielded no differences for any measured microhabitat variable: vegetation richness ($p=0.43$), the percent of canopy open ($p=0.89$), horizontal cover by ground level vegetation ($p=0.33$), horizontal cover by short vegetation ($p=0.72$) and horizontal cover by tall vegetation ($p=0.17$; Table 2.10).

Nest Surveillance and Success

During the 2009 breeding season, observers detected and video monitored five nests at Mackay Island NWR, and two nests at Back Bay NWR (Figure 2.5). Of these nests, six were located in 0 YSB habitat, and one was located in 2 YSB habitat (Figure 2.6). The earliest nest detection was 4 May, and the latest nest detection was 2 June. The last nest finished on 17 June (Table 2.11). Four nests were successful, two failed due to raccoon (*Procyon lotor*) or black rat snake (*Elaphe obsoleta obsoleta*) predation, and one had an unknown fate (Appendix C).

During the 2010 breeding season, observers detected nine nests at Mackay Island NWR, and video monitored seven of these nests (Figure 2.7). Nest detections occurred during the second or third search and in seven of the fourty-one survey plots, with two plots containing two nests. Four nests were located in 0 YSB, four were located in 1 YSB, and one was located in 2 YSB (Figure 2.8). The earliest nest detection was 22 May, and the latest nest detection was 11 June. The last nest finished on 1 July (Table 2.11). Five monitored nests were successful. Two monitored nests failed by either raccoon or black rat snake predation (Appendix C). The two unmonitored nests had unknown fates.

The average clutch size of King Rails in this study was 9.64 ± 0.58 eggs; the average incubation period was 21 days. A model with constant survival over the season best explained nest survival for nests during the entire egg stage (AICw = 0.33; Table 2.12). Plausible alternatives ($\Delta\text{AIC} \leq 2$) included models that featured linear (T), quadratic (TT), and year (2009-2010) terms. Estimated daily survival rate $\widehat{DSR}$ among competing models ranged from 0.961 to 0.983, with a lower 95% CI ranging from 0.774 to 0.937 and an upper 95% CI ranging from 0.993 to 0.995. The estimated probability of a nest surviving the egg stage (31 d) was 0.48 (95% CI = 0.056 - 0.826).

A model with *timeaway* as a covariate best explained nest survival for the incubation stage (AICw = 0.70; Table 2.13). $\widehat{DSR}$ was 0.970 ± 0.022, and $\widehat{PSR}$ was 0.538. The time nests were left unattended had a strong negative influence on nest survival (*timeaway* β = -1.89 ± 0.83; Figure 2.9). The time parents spent maintaining the nest also had a negative but weak influence on nest survival ($fixveg$ β = -0.43 ± 0.65; Figure 2.10). There was no difference in the mean daily duration of nest maintenance on days when vegetation was trimmed (81.09 s ± 18.26 s) when compared to other days during the incubation period (91.01 s ± 8.68 s; p=0.63).

2.6 Discussion

I estimated the probability of occupancy after adjusting for detection probability, as well as the probability of detecting reproductive activity at occupied sites for King Rails in Southern Virginia/Northeastern North Carolina. Occupancy and abundance are often used to infer habitat quality; however, they are not always positively correlated, prompting the need to define habitat quality based on measures of fitness (Van Horne 1983). This is the the first study in rail literature that attempts to link site occupancy to vital parameters through a related metric, the probability of reproductive activity. The multi-state modeling framework used in this study also provided a basis to test the influence of habitat variables on measures of site productivity, and can be useful for informing management or conservation decisions (Martin et al. 2009; Nichols et al. 2007). All together, the approach followed in this study provided an example of a more comprehensive assessment of species distribution models (SDM), which seek to gain a greater understanding about how habitat quantity and quality influence biological processes, and ultimately, a species' abundance and distribution (Wiens, Stenseth, Van Horne & Ims 1993).

Time since marsh burn emerged as a factor that influences all parameters favorably. King Rails occurred and nested in recently burned marsh plots with greater probability than in non-recently burned marsh plots. Moreover, the proportion of nests in these sites could not be explained by random site selection based on habitat availability. Unfortunately, the relationship between nest success (egg stage) and time since burn categories could not be determined, because the sample size of nests was too small. This precluded establishing linkages between nest success and occupancy in burned plots of different burn histories. Therefore, future studies should address this research need as it has major implications with regards to understanding rail habitat quality (Van Horne 1983). In this vein, and perhaps a more useful expression of breeding productivity, brood survival could also be influenced by burn history. Studies have shown that King Rail broods require shallow water for foraging and sufficient vegetation cover for concealment from predators (Darrah 2008; Reid 1989). However, the effect of prescribed burns on brood survival of rails has not been explored. Studies of other avian taxa (*e.g.*, sparrows, ducks) suggest that nest or brood survival was not affected by burns (Gabrey, Wilson & Afton 2002). Actually, some studies suggested that burned habitats provide greater food availability and allowed for increased movement away from predators (Gabrey et al. 2002; Johnson & Temple 1990; Patten, Shochat, Wolfe & Sherrod 2007).

At the scale of survey plots, I could not detect differences in microhabitat measurements, nor discern the benefits or disadvantages of prescribed burns on nest site selection. Although microhabitat variables (*e.g.*, cover, water depth) have been found to be important determinants for nest-site selection among marsh birds, interspecific interactions including predation may also play a role in selecting nest sites (Lor & Malecki 2006). For instance, nest placement in marshes with greater average water depths limits raccoon access and has been found to increase nest success of waterfowl (Jobin & Picman 1997; Urban 1970). Nest predators react to many habitat variables; however, and patterns of these responses occur at multiple scales, from patch to landscape (Klug et al. 2009). King Rail nest placement with respect to prescribed burns may also operate at a larger scale than was considered in this study.

This study augmented the knowledge about King Rail breeding ecology and the factors impinging on nest success. Average clutch size and length of incubation are similar to previous estimations for King Rails (Meanley 1969; Poole et al. 2005; Reid 1989). However, this is the first study that quantified King Rail parental behavior during incubation through the use of continuous video monitoring. Although raccoons are commonly documented predators at King Rail nests (Meanley 1969; Poole et al. 2005; Reid 1989), this study confirmed the importance of black rat snakes as nest predators. Both predators were documented destroying nests and leaving nests intact, suggesting that is is hard to discern cause of nest failure by solely inspecting nest conditions. Video monitoring also provided a basis for insights on the effects of human visitation to monitor nests. Parent rails often flushed when observers approached the nest to trim vegetation, an activity to maintain clear field of view for the video camera. Conversely, parents did not engage on activities or increase any activity that would be construed as increased nest maintenance due to clearance of vegetation. Clearly, disturbance by human activity could increase vulnerability of nests (*e.g.*, nest attentiveness). It is also noteworthy that trails were created leading to and from the monitoring system, which might provide access by predators. The effect of these trails on nest success, however, was not explicitly accounted for in this study. Indirectly, trails became more distinct throughout the survey period, and time covariates for daily survival rate may have incorporated any effects of these developing trails. This should be kept in mind when interpreting results from nest success (egg stage) presented below.

The estimated probability of nest success for the egg stage reported here was lower than for other studies looking at the same stage (Pierluissi 2006; Reid 1989). For 59 King Rail nests in Louisiana rice fields, Pierluissi (2006) calculated daily survival rates of 0.979 ± 0.006 and 0.977 ± 0.007 for the study years, which correspond to period survival rates of 0.521 and 0.503, respectively. For 67 nests in Missouri managed wetlands, Reid (1989) calculated a daily survival rate of 0.971 and a period survival rate of 0.695 ± 0.071. The probability of nest success for the incubation stage was closer to those reported by other studies because I excluded nests that failed during egg laying. The low sample size of nests in this analysis made the estimates more sensitive to the addition of failed nests, which may account for the discrepancy among results. Furthermore, nest success is difficult to generalize across a species' range due to differences in habitat conditions and nest predators (Morrison, Marcot & Mannan 2006). For example, in this study fire management and predation by snakes stood out as factors that might contribute to site-specific differences when compared to other studies. As noted above, it is possible that my estimates are slightly biased low due to human visitation during video monitoring.

Nest survival models during the incubation stage permitted the assessment of the influence of parental behavior on nest success. I found that the amount of time away from the nest had a negative influence on success. This finding is supported by previous work that showed that decreased nest attentiveness may increase the risk of predation (Fontaine et al. 2007). Factors that might influence time away from the nest include levels of food availability. Parents may spend more time away from the nest if availability of resources is low, which might lead to decreased foraging efficiency (Martin 1987). In addition to the effects on incubation, low food availability can also decrease brood and adult survival (Martin 1987). This possible relationship between resource base, availability and fire management is important and deserves attention in future studies because evidence from this study suggested that structural characteristics at the plot level between recently and non-recently burned habitat were not statistically different.

This study was designed to supplement a broader project aimed at stepping-down population and habitat objectives for King Rails in the Southeast (Drew et al. 2006; Hunter et al. 2006). This study more thoroughly connected these objectives by addressing current management actions and King Rail responses to those actions that are related to fitness. Fire management did not adversely affect occurrence or reproductive activity of King Rails at Mackay Island NWR and Back Bay NWR. However, I recommend that demographic parameters at other management units be assessed in a similar fashion before results are generalized and used to inform management decisions. Such efforts should adjust occupancy and reproductive activity estimates for detection probability in order to draw stronger inferences about rail-habitat relationships and allow comparisons across multiple sites (MacKenzie et al. 2006).

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Table 2.1: Encounter histories coded in PRESENCE in detection-non-detection format to model multi-state occupancy.

Site ID	Survey 1	Search 1	Survey 2	Search 2	Survey 3	Search 3
621378	0	0	0	0	0	0
622650	0	0	0	0	0	0
622651	0	0	0	0	0	0
622664	0	0	0	0	0	0
622668	0	0	0	0	0	0
626280	1	0	1	0	1	0
626281	1	0	1	0	1	0
626876	1	0	1	0	1	0
626877	1	0	1	0	1	0
626878	0	0	0	0	0	0
627464	1	0	0	0	0	0
628051	1	0	1	0	0	0
628053	0	0	0	0	0	0
629200	0	0	0	0	0	0
629201	0	0	0	0	0	0
629215	1	0	0	0	1	0
629788	1	0	1	0	0	2
629789	0	0	1	0	0	0
630345	1	0	0	2	0	0
630350	1	0	1	0	1	0
630914	1	0	1	0	1	0
630915	1	0	0	2	1	2
630957	1	0	0	0	1	0
631474	1	0	1	0	1	0
632075	0	0	0	0	0	0
632077	0	0	0	0	0	0
633140	1	0	1	0	0	2
633177	1	0	1	0	1	0
633178	1	0	1	0	0	0
633689	1	0	1	2	1	2
633690	0	0	1	0	1	2
633722	1	0	1	0	0	0
633724	0	0	1	0	1	0

Table 2.1: (continued)

Site ID	Survey 1	Search 1	Survey 2	Search 2	Survey 3	Search 3
634265	0	0	0	0	0	0
634266	0	0	0	0	0	0
634779	0	0	0	0	0	0
635317	1	0	1	0	1	0
635319	0	0	1	2	1	2
999991	0	0	0	0	0	0
999992	0	0	0	0	0	0
999993	0	0	0	0	1	0

Table 2.2: Site covariates for occupancy and reproductive activity used to model multi-state occupancy in PRESENCE. Location refers to survey plot placement at Mackay Island NWR.

Site ID	Burn	Edge	Depth	Salinity	Location
621378	0	0	1.000	6.600	0
622650	1	0	1.000	6.467	0
622651	0	1	0.667	10.615	0
622664	0	0	0.083	48.333	0
622668	0	0	1.538	16.200	0
626280	0	0	0.714	19.143	1
626281	0	0	0.385	21.867	1
626876	0	0	0.077	16.600	1
626877	0	0	0.571	9.133	1
626878	0	0	0.444	6.533	1
627464	0	0	0.200	15.286	1
628051	0	0	1.133	10.733	1
628053	0	0	0.750	15.800	1
629200	1	1	0.455	10.714	1
629201	0	0	1.286	4.643	1
629215	0	0	1.333	7.333	1
629788	1	1	1.700	9.286	1
629789	1	1	1.133	19.267	1
630345	1	1	0.818	14.308	1
630350	1	0	1.111	4.467	1
630914	1	0	1.000	11.133	1
630915	1	0	0.333	9.000	1
630957	0	0	1.600	6.786	0
631474	1	0	0.231	8.867	1
632075	0	0	2.000	4.933	0
632077	0	0	0.000	1.467	0
633140	1	0	0.600	8.133	1
633177	1	0	0.500	2.000	0
633178	1	0	1.100	5.600	0
633689	1	1	0.733	30.533	1
633690	1	1	1.214	4.333	1
633722	0	0	0.625	8.367	0
633724	1	1	0.875	4.600	0

Table 2.2: (continued)

Site ID	Burn	Edge	Depth	Salinity	Location
634265	0	0	5.600	3.818	0
634266	0	0	2.556	4.333	0
634779	0	0	0.429	15.667	1
635317	0	0	3.000	0.467	1
635319	0	0	0.429	13.467	1
999991	0	0	0.667	4.500	0
999992	0	0	0.111	7.867	0
999993	0	0	0.400	9.067	0

Table 2.3: Sampling covariate accounting for the presence of active nests over multiple surveys used multi-state occupancy models in PRESENCE.

Site ID	Nest 1	Nest 2	Nest 3
621378	0	0	0
622650	0	0	0
622651	0	0	0
622664	0	0	0
622668	0	0	0
626280	0	0	0
626281	0	0	0
626876	0	0	0
626877	0	0	0
626878	0	0	0
627464	0	0	0
628051	0	0	0
628053	0	0	0
629200	0	0	0
629201	0	0	0
629215	0	0	0
629788	0	0	0
629789	0	0	0
630345	0	0	0
630350	0	0	0
630914	0	0	0
630915	0	0	1
630957	0	0	0
631474	0	0	0
632075	0	0	0
632077	0	0	0
633140	0	0	0
633177	0	0	0
633178	0	0	0
633689	0	0	1
633690	0	0	0
633722	0	0	0
633724	0	0	0

Table 2.3: (continued)

Site ID	Nest 1	Nest 2	Nest 3
634265	0	0	0
634266	0	0	0
634779	0	0	0
635317	0	0	0
635319	0	0	1
999991	0	0	0
999992	0	0	0
999993	0	0	0

Table 2.4: Model notation for a set of candidate models for single season multi-state analysis.

Model Notation	Parameter Description
$\Psi^1(.)$	The probability of site occupancy is constant.
$\Psi^1(location)$	The probability of site occupancy depends on the refuge in which the survey plot is located. This covariate encapsulates differences between refuges due to geographic location, as well as differences in attributes inherent to each refuge measured in this study, including marsh type (*i.e.*, natural or impounded) and patch size.
$\Psi^1(burn)$	The probability of site occupancy depends on the presence of recently burned habitat at the center of the survey plot.
$\Psi^1(location + burn)$	The probability of site occupancy depends on the refuge in which the survey plots was located and the presence of recently burned habitat at the center of the survey plot.
$\Psi^1(edge)$	The probability of site occupancy depends on the presence of an interface between recently burned and non-recently burned habitat within the 200 m radius survey plot.
$\Psi^1(salinity)$	The probability of site occupancy depends on the mean salinity within the 200 m radius survey plot.
$\Psi^1(depth)$	The probability of site occupancy depends on the mean water depth within the 200 m radius survey plot.
$\Psi^2(.)$	The probability of reproduction is constant.
$\Psi^2(location)$	The probability of reproduction depends on the refuge in which the survey plot is located. This covariate encapsulates differences between refuges due to geographic location, as well as differences in attributes inherent to each refuge measured in this study, including marsh type (*i.e.*, natural or impounded) and patch size.

Table 2.4: (continued)

Model Notation	Parameter Description
$\Psi^2(burn)$	The probability of reproduction depends on the presence of recently burned habitat at the center of the survey plot.
$\Psi^2(location + burn)$	The probability of reproduction depends on the refuge in which the survey plot is located and the presence of recently burned habitat at the center of the survey plot.
$\Psi^2(edge)$	The probability of reproduction depends on the presence of an interface between recently burned and non-recently burned habitat within the 200 m radius survey plot.
$\Psi^2(salinity)$	The probability of reproduction depends on the mean salinity within the 200 m radius survey plot.
$\Psi^2(depth)$	The probability of reproduction depends on the mean water depth within the 200 m radius survey plot.
$p^1(.)$	The probability of detection during a call-broadcast is constant.
$p^1(t)$	The probability of detection during a call-broadcast is survey-dependent.
$p^1(burn)$	The probability of detection during a call-broadcast depends on the presence of recently burned habitat at the center of the survey plot.
$p^1(location)$	The probability of detection during a call-broadcast depends on the refuge in which the survey plot is located.
$p^2(.)$	The probability of detecting a nest during a nest search is constant.

Table 2.4: (continued)

Model Notation	Parameter Description
$p^2(t)$	The probability of detecting a nest during a nest search is survey-dependent.
$p^2(nest)$	The probability of detecting a nest during a nest search depends on whether the location of an active nest is previously known.
$p^2(burn)$	The probability of detecting a nest during a nest search depends on the presence of recently burned habitat at the center of the survey plot.
$p^2(location)$	The probability of detecting a nest during a nest search depends on the refuge in which the survey plot is located.
$\delta(.)$	The probability of correct assignment into a breeding state given the site was occupied and King Rails were detected is constant. For call-broadcast surveys, δ^1 is fixed to zero. For nest searches, δ^2 is fixed to one.

Table 2.5: Mean daily durations of parental absence from the nest and parental time spent fixing vegetation during the incubation period for nests found in 2009 and 2010 breeding seasons. Means are calculated from all full days of video data.

Nest	Mean Daily Time Away (s)	Mean Daily Fixing Vegetation (s)
2010_MI02	748	1174
2010_MI03	1907	413
2010_MI04	2076	3431
2010_MI05	3750	678
2010_MI06	1491	1019
2010_MI08	742	33
2010_MI09	280	749
2009_MI04	2973	241
2009_MI06	1790	2200
2009_MI08	691	1581
2009_BB01	923	27
2009_BB02	527	681

Table 2.6: Model notation for MARK nest survival candidate models for 2009 and 2010 King Rail nests.

Model Notation	Parameter Description
$S(T)$	The probability of nest survival is linearly dependent on time.
$S(TT)$	The probability of nest survival is quadratically dependent on time.
$S(g)$	The probability of nest survival is year-dependent.
$S(T+g)$	The probability of nest survival is linearly time-dependent and year-dependent.
$S(TT+g)$	The probability of nest survival is quadratically time-dependent and year-dependent.
$S(.)$	The probability of nest survival is constant.
$S(timeaway)$	The probability of nest survival is dependent on the mean daily duration of parent absence from nest.
$S(fixveg)$	The probability of nest survival is dependent on the mean daily duration of a parent fixing vegetation around the nest.

Table 2.7: A set of candidate models for single season multi-state analysis ranked by their associated AIC values.

Model	AIC	ΔAIC	AICw	Model Likelihood	Parameters	–2Log Likelihood
$\Psi^1(burn + location), \Psi^2(burn + location), p^1(.), p^2(nest), \delta(.)$	185.60	0.00	0.9197	1.0000	10	165.60
$\Psi^1(burn + location), \Psi^2(burn + location), p^1(.), p^2(.), \delta(.)$	190.56	4.96	0.0770	0.0837	9	172.56
$\Psi^1(burn), \Psi^2(burn), p^1(.), p^2(.), \delta(.)$	198.26	12.66	0.0016	0.0018	8	182.26
$\Psi^1(location), \Psi^2(location), p^1(.), p^2(.), \delta(.)$	198.37	12.77	0.0016	0.0017	8	182.37
$\Psi^1(edge), \Psi^2(edge), p^1(.), p^2(.), \delta(.)$	204.73	19.13	0.0001	0.0001	8	188.73
$\Psi^1(.), \Psi^2(.), p^1(.), p^2(.), \delta(.)$	207.90	22.30	0.0001	0.0001	7	193.90
$\Psi^1(.), \Psi^2(.), p^1(location), p^2(location), \delta(.)$	207.95	22.35	0.0000	0.0000	6	195.95
$\Psi^1(depth), \Psi^2(depth), p^1(.), p^2(.), \delta(.)$	208.96	23.36	0.0000	0.0000	8	192.96
$\Psi^1(.), \Psi^2(.), p^1(burn), p^2(rburn), \delta(.)$	209.04	23.44	0.0000	0.0000	6	197.04
$\Psi^1(salinity), \Psi^2(salinity), p^1(.), p^2(.), \delta(.)$	209.62	24.02	0.0000	0.0000	8	193.62
$\Psi^1(.), \Psi^2(.), p^1(t), p^2(t), \delta(.)$	210.08	24.68	0.0000	0.0000	5	200.18

Table 2.8: Area of habitat searched in 2010 by fire management history (YSB) and percent of available habitat of each fire history during the breeding season. Area searched includes all survey plots from Back Bay NWR and Mackay Island NWR.

YSB	Area Searched (ha)	Percent of Habitat
0	68.35	0.142
1	99.13	0.206
2	48.31	0.101
≥ 3	264.86	0.652

Table 2.9: Mean measurements for microhabitat variables considered in 2010 analyses for sites where a nest was found (n=9) and sites where no nest was found (n=41). Sites were compared using 2-sample t-tests. Horizontal cover measurements consider vegetation cover by ground cover (< 0.5 m), cover by short vegetation (< 1 m) and cover by tall vegetation (> 1 m). Estimates are reported with standard errors (± SE).

Microhabitat Variable	Nest Found	No Nest Found	P=value
Vegetation Richness	5.78 ± 0.36	5.68 ± 0.41	p=0.86
Percent of Canopy Open	32.93 ± 13.89	23.4 ± 5.28	p=0.54
Percent of Horizontal Cover (< 0.5 m)	100.00 ± 0.00	95.38 ± 2.62	p=0.09
Percent of Horizontal Cover (< 1 m)	92.82 ± 4.52	84.83 ± 3.83	p=0.19
Percent of Horizontal Cover (> 1 m)	16.20 ± 7.14	36.53 ± 5.29	p=0.03

Table 2.10: Mean measurements for microhabitat variables considered in 2010 analyses for recently burned sites where a nest was found (n=8) and recently burned sites where no nest was found (n=15). Sites were compared using 2-sample t-tests. Horizontal cover measurements consider vegetation cover by ground cover (< 0.5 m), cover by short vegetation (< 1 m) and cover by tall vegetation (> 1 m). Estimates are reported with standard errors (± SE).

Microhabitat Variable	Nest Found	No Nest Found	P=value
Vegetation Richness	5.63 ± 0.38	6.33 ± 0.79	p=0.43
Percent of Canopy Open	26.52 ± 13.97	24.27 ± 9.12	p=0.89
Percent of Horizontal Cover (< 0.5 m)	100.00 ± 0.00	97.64 ± 2.36	p=0.33
Percent of Horizontal Cover (< 1 m)	92.45 ± 5.11	89.79 ± 5.25	p=0.72
Percent of Horizontal Cover (> 1 m)	17.32 ± 8.00	34.58 ± 9.25	p=0.17

Table 2.11: King Rail nests found at Mackay Island NWR and Back Bay NWR during 2009 and 2010 breeding seasons. All known outcomes were documented using video surveillance. For nests not monitored by video surveillance, dates of nest visits are listed. Nests are listed in order of discovery.

Nest ID	Dates Monitored	Eggs When Found	Total Eggs Laid	Outcome
2009_MI01	5/04/09-5/07/09	2	3	Failure
2009_BB01	5/05/09-6/11/09	8	10	Success
2009_MI04	5/16/09-5/28/09	8	8	Success
2009_BB02	5/19/09-6/02/09	12	12	Success
2009_MI06	5/21/09-6/16/09	6	11	Failure
2009_MI08	6/01/09-6/17/09	12	12	Success
2009_MI09	6/02/09-6/03/09	4	4	Unknown
2010_MI01	5/22/10-5/27/10	3	5	Failure
2010_MI02	5/22/10-6/28/10	3	7	Success
2010_MI03	5/27/10-6/23/10	6	7	Success
2010_MI04	5/27/10-6/18/10	9	9	Success
2010_MI05	6/01/10-6/05/10	9	9	Failure
2010_MI06	6/05/10; 6/29/10	8	-	Unknown
2010_MI07	6/10/10	7	-	Unknown
2010_MI08	6/11/10-7/01/10	12	12	Success
2010_MI09	6/11/10-6/19/10	9	9	Success

Table 2.12: MARK nest survival candidate models for 2009 and 2010 King Rail nests that were monitored during the egg stage (n=14), which includes egg laying and incubation. Models are ranked by their associated AIC values.

Model	AICc	ΔAICc	AICc wgt	Model Likelihood	Parameters	Deviance
$S(.)$	40.8223	0.0000	0.32938	1.0000	1	38.8010
$S(T)$	41.4208	0.5985	0.24419	0.7414	2	37.3566
$S(TT)$	42.5718	1.7495	0.13734	0.4170	3	36.4427
$S(g)$	42.8100	1.9877	0.12192	0.3701	2	38.7459
$S(T+g)$	43.0882	2.2659	0.10609	0.3221	3	36.9592
$S(TT+g)$	44.1924	3.3701	0.06108	0.1854	4	35.9762

Table 2.13: MARK nest survival candidate models for 2009 and 2010 King Rail nests that were monitored during the incubation period (n=12) ranked by their associated AIC values.

Model	AICc	ΔAICc	AICc wgt	Model Likelihood	Parameters	Deviance
$S(timeaway)$	20.2824	0.0000	0.7037	1.0000	2	16.2106
$S(.)$	23.7708	3.4884	0.1230	0.1748	1	21.7470
$S(fixveg)$	25.4132	5.1308	0.0541	0.0769	2	21.4313
$S(T)$	25.5284	5.2460	0.0511	0.0726	2	21.4566
$S(g)$	25.7709	5.4885	0.0453	0.0643	2	21.6991
$S(T+g)$	27.1345	6.8521	0.0229	0.0325	3	20.9899

Figure 2.1: The study region includes marsh habitat located in Southeastern Virginia and Northeastern North Carolina at Back Bay National Wildlife Refuge, False Cape State Park and Mackay Island National Wildlife Refuge.

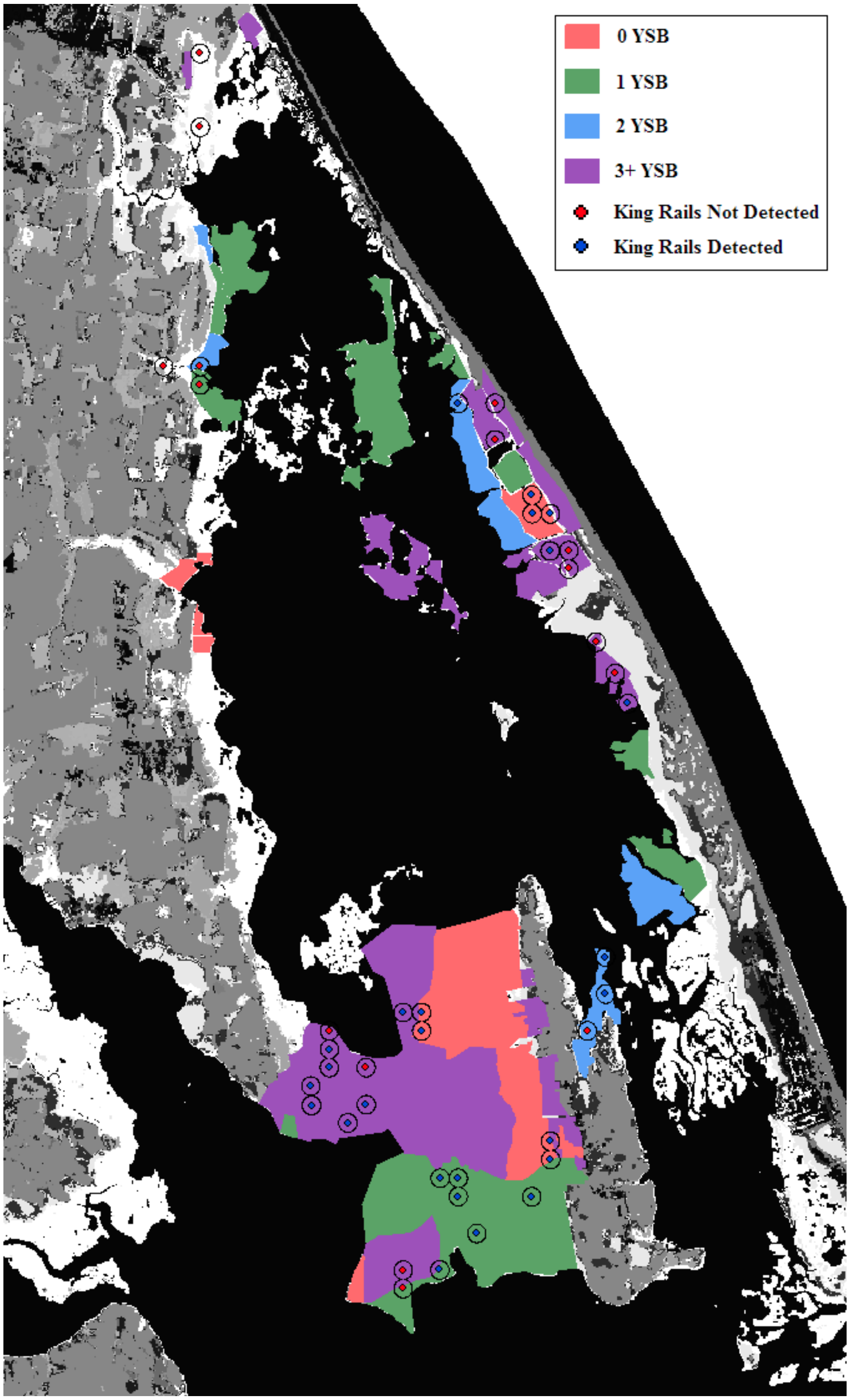


Figure 2.2: Call-broadcast survey site locations and detections at Mackay Island NWR, Back Bay NWR and False Cape State Park during the 2010 breeding season. The study area is colored according to fire management history, and sites are colored by detections. Sites were selected from a systematic grid overlaying marsh habitat such that points were spaced 400 m apart. Sites are shown with 200 m buffers.

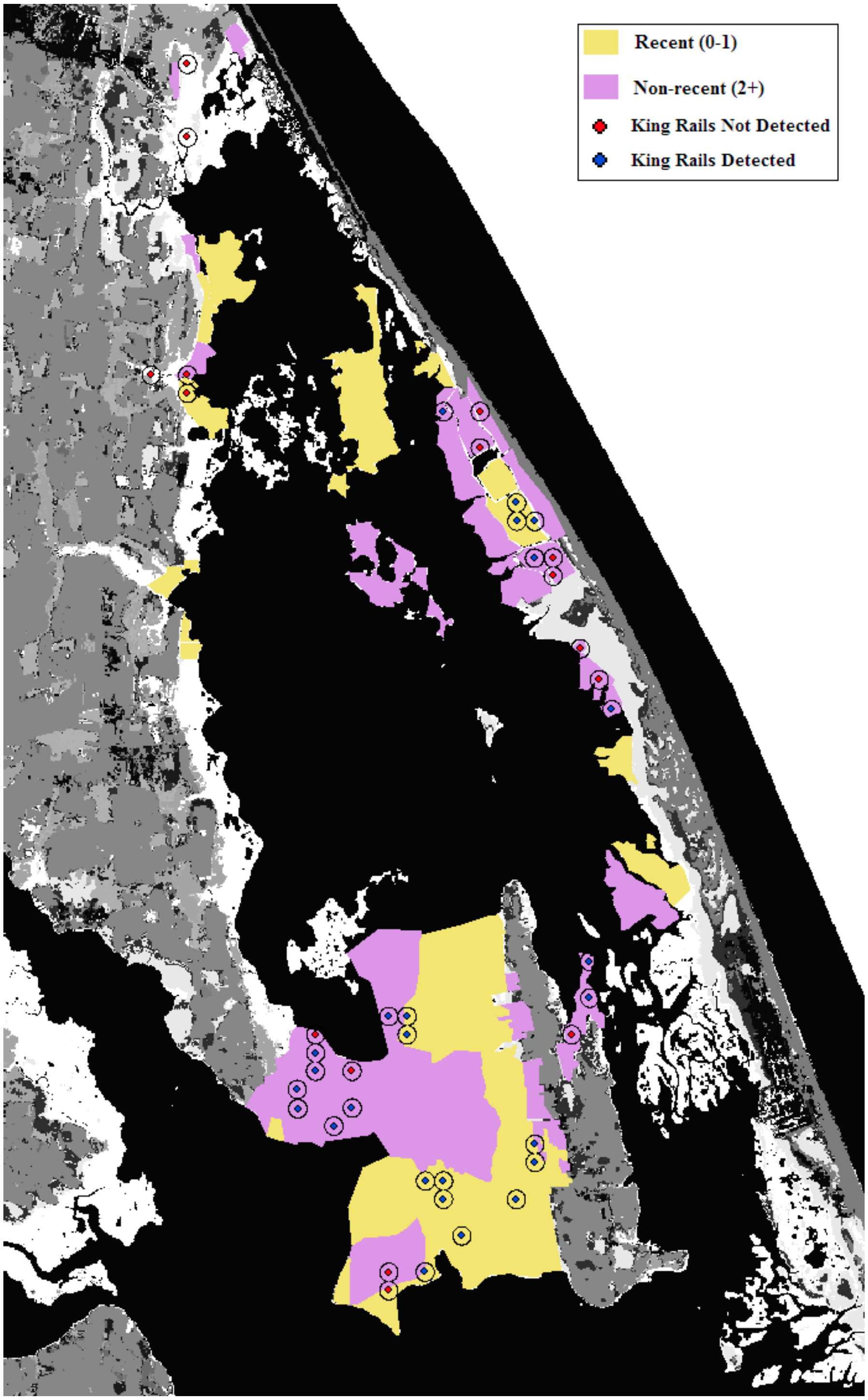


Figure 2.3: Call-broadcast survey site locations and detections at Mackay Island NWR, Back Bay NWR and False Cape State Park during the 2010 breeding season. The study area is colored by recent (0-1 YSB) and non-recent (≥2 YSB) burns, and sites are colored by detections. Sites were selected from a systematic grid overlaying marsh habitat such that points were spaced 400 m apart. Sites are shown with 200 m buffers.

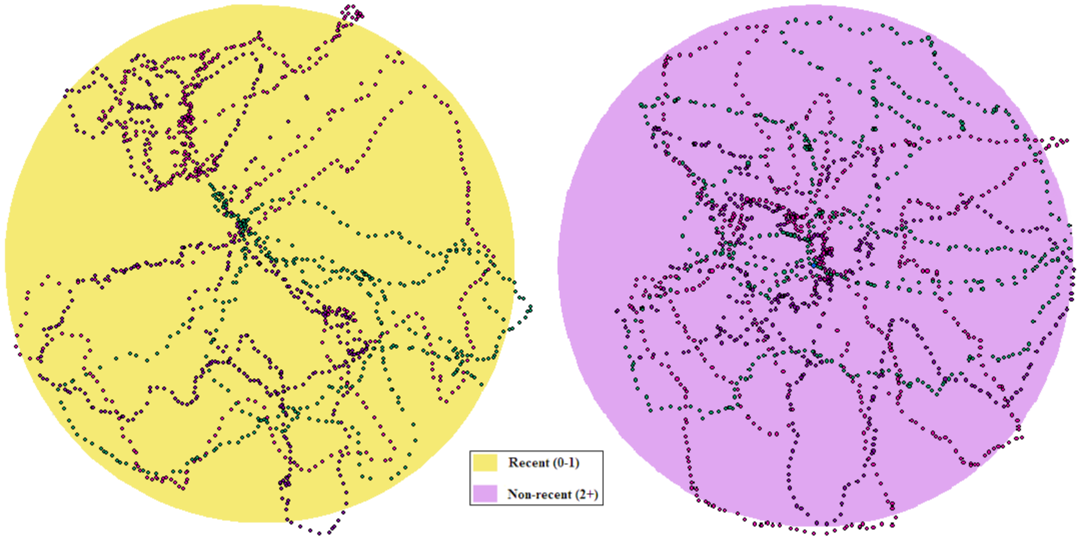


Figure 2.4: Example search tracks for recently burned (0-1 YSB) and non-recently (≥2 YSB) burned plots. All search tracks recorded during the breeding season for each plot are shown. Non-recently burned plots were searched as thoroughly as recently burned plots.

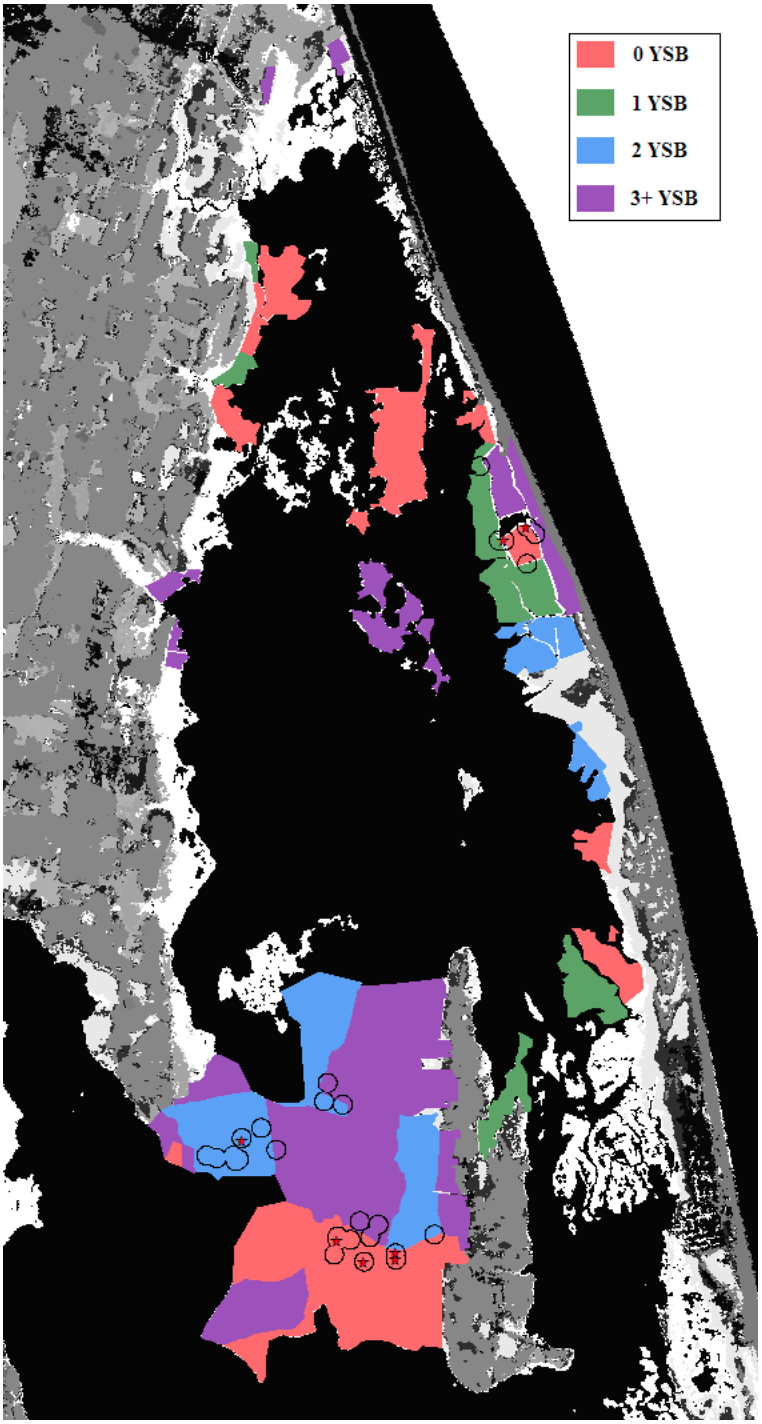


Figure 2.5: Area searched and King Rail nests found at Mackay Island NWR and Back Bay NWR during the 2009 breeding season. The study area is colored according to fire management history.

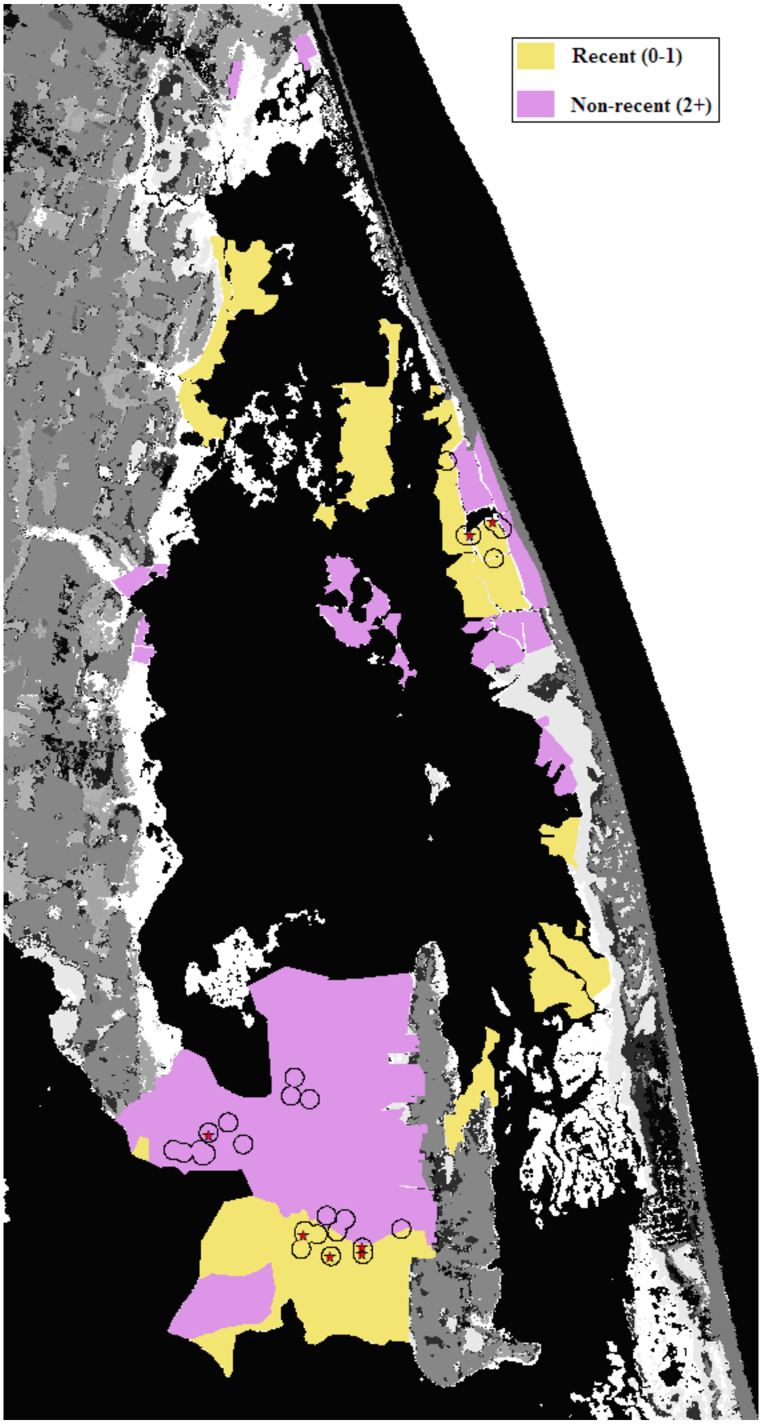


Figure 2.6: Area searched and King Rail nests found at Mackay Island NWR and Back Bay NWR during the 2009 breeding season. The study area is colored by recent (0-1 YSB) and non-recent (≥2 YSB) burns.

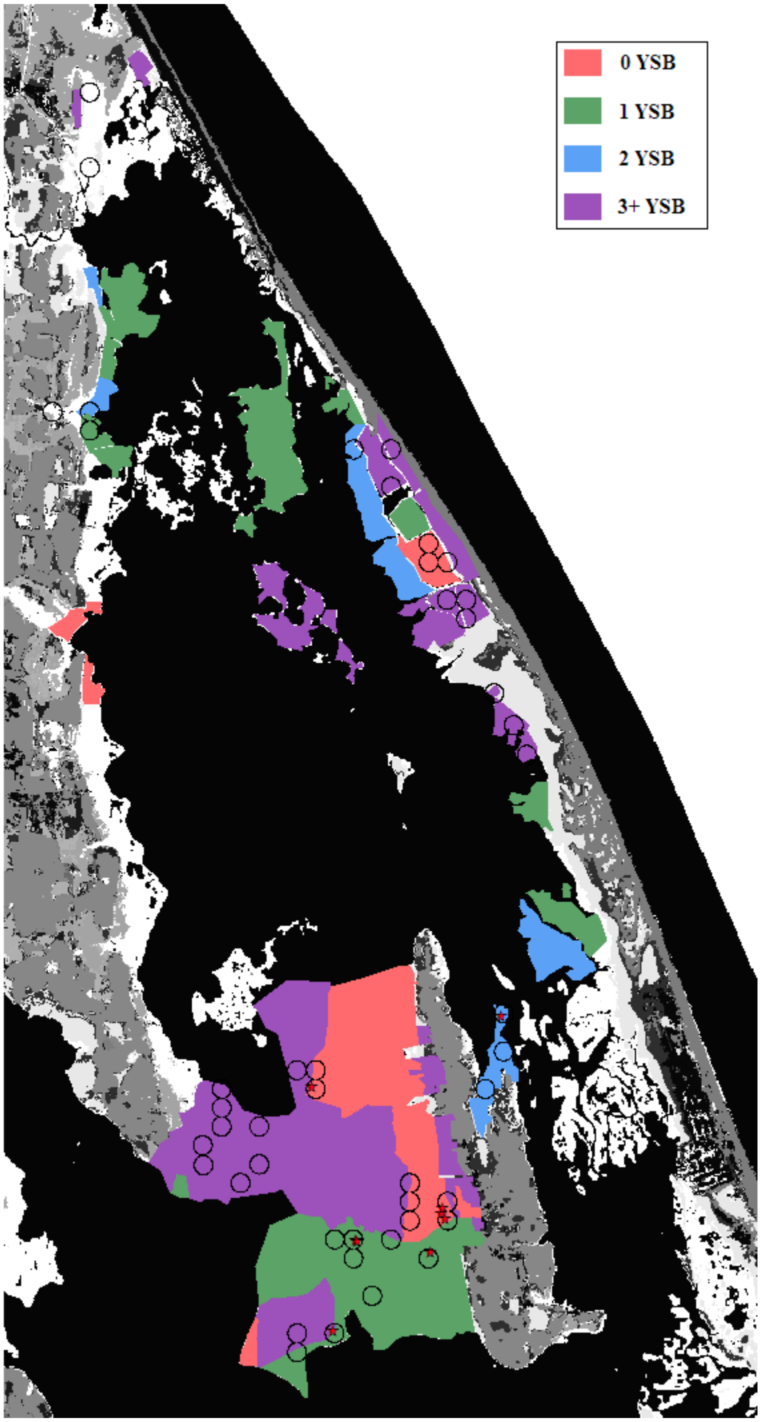


Figure 2.7: Area searched and King Rail nests found at Mackay Island NWR, Back Bay NWR, and False Cape State Park during the 2010 breeding season. The study area is colored according to fire management history.

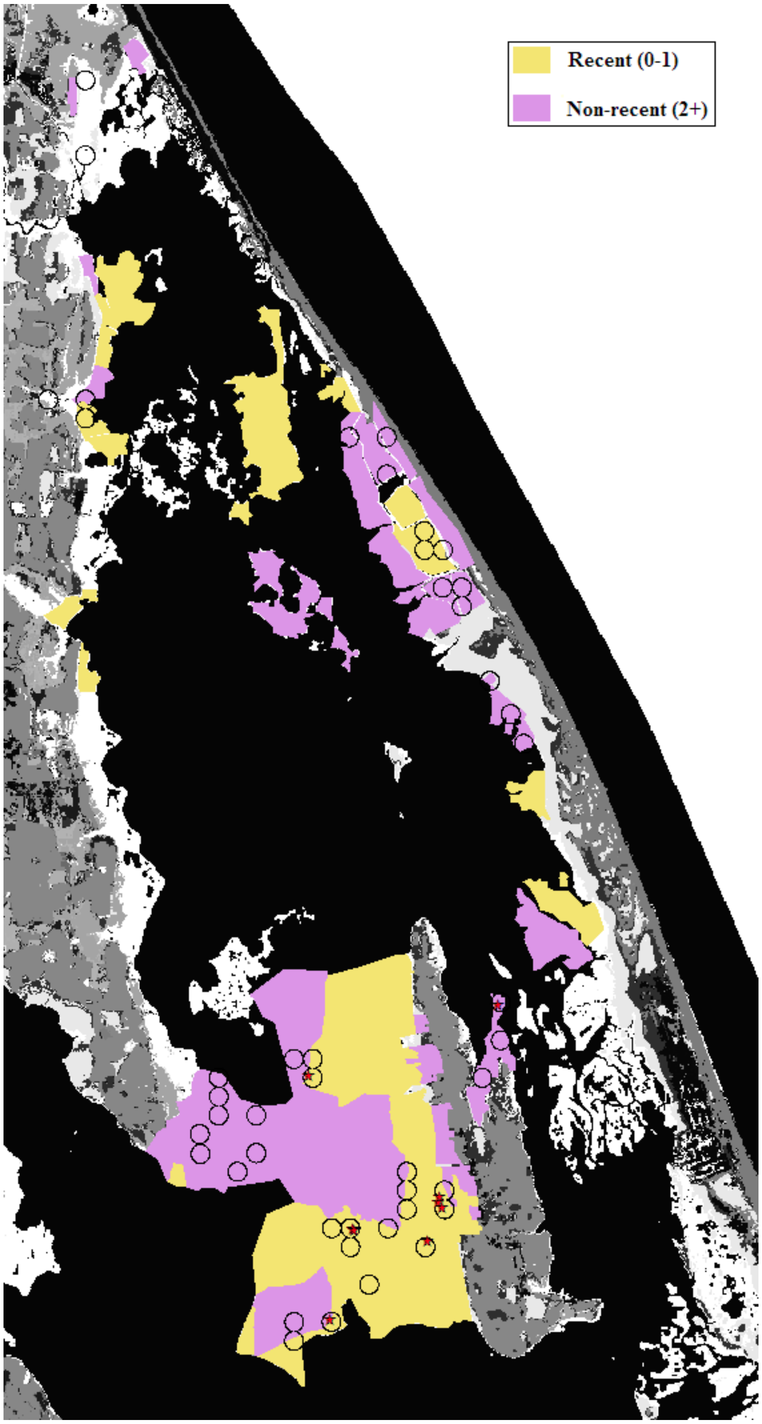


Figure 2.8: Area searched and King Rail nests found at Mackay Island NWR, Back Bay NWR, and False Cape State Park during the 2010 breeding season. The study area is colored by recent (0-1 YSB) and non-recent (≥2 YSB) burns.

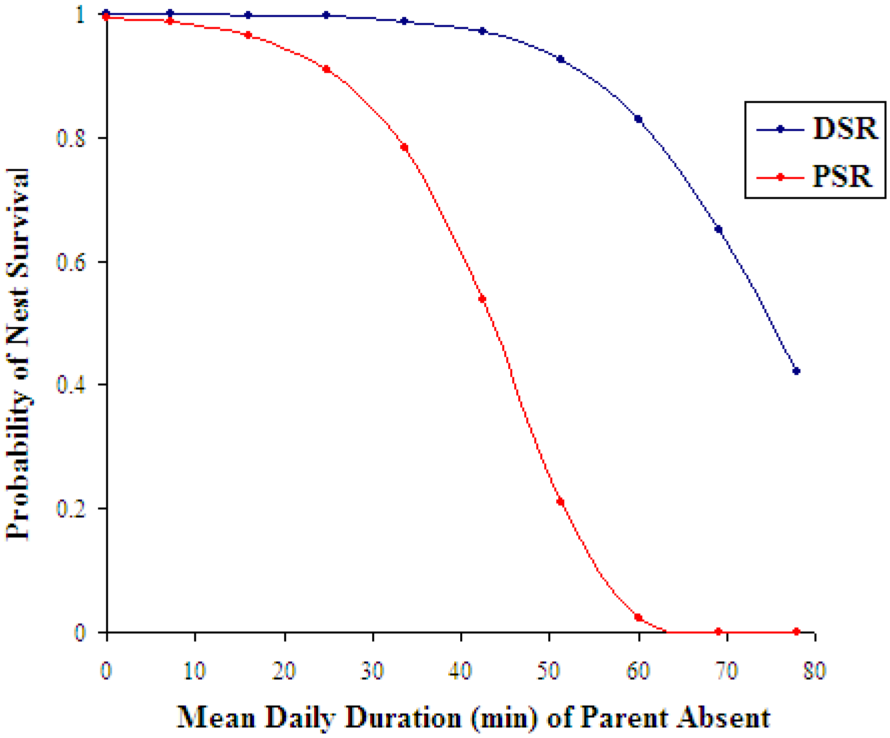


Figure 2.9: The amount of time a parent spends away from the nest during the incubation period has a strong negative influence on daily nest survival (DSR) and period nest survival (PSR).

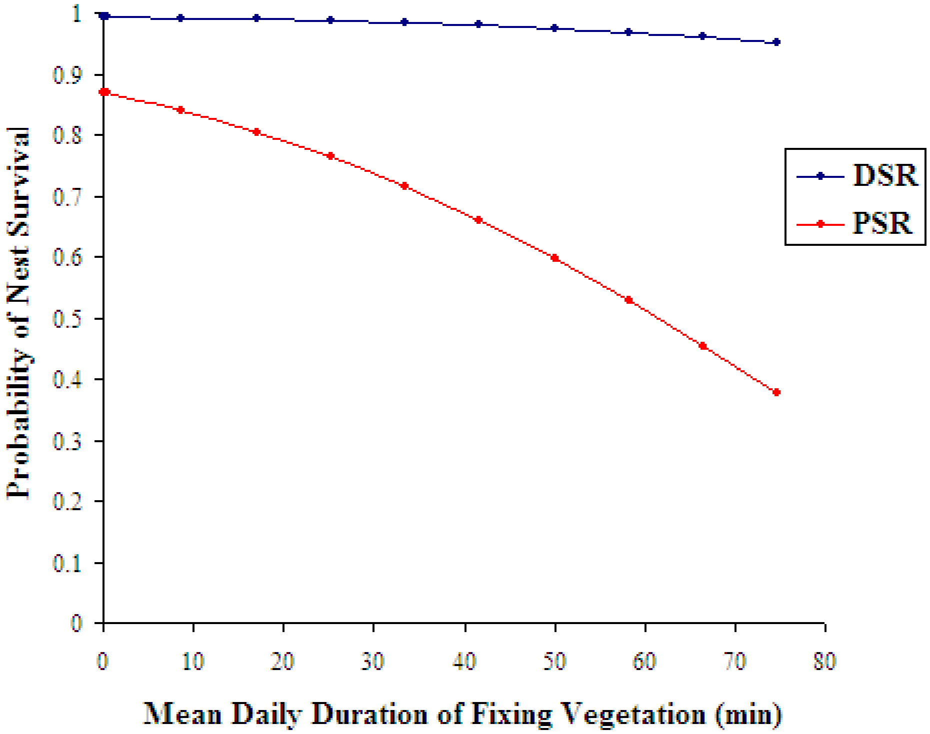


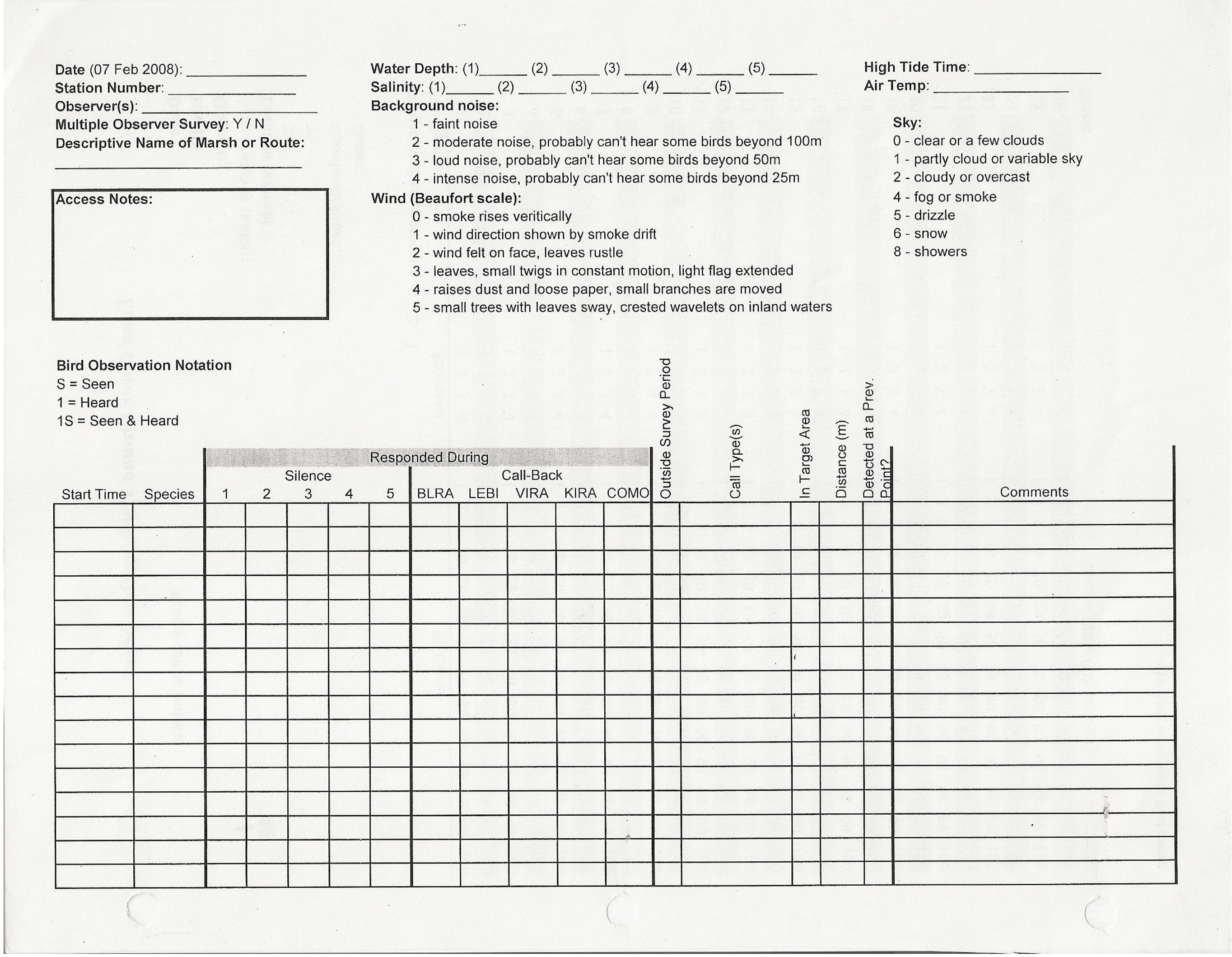
Figure 2.10: The amount of time a parent spends fixing vegetation around the nest during the incubation period has a weak negative influence on daily nest survival (DSR) and period nest survival (PSR).

APPENDICES

Appendix A

Field Data

The following data sheets were used during the 2010 field season to record King Rail detections during call-broadcast surveys, measurements of microhabitat and descriptions of nest visits.



Date (07 Feb 2008): _______________
Station Number: _______________
Observer(s): _______________
Multiple Observer Survey: Y / N
Descriptive Name of Marsh or Route:
____

Access Notes:

Water Depth: (1)______ (2) ______ (3) ______ (4) ______ (5) ______
Salinity: (1)______ (2) ______ (3) ______ (4) ______ (5) ______

Background noise:

1 - faint noise
2 - moderate noise, probably can't hear some birds beyond 100m
3 - loud noise, probably can't hear some birds beyond 50m
4 - intense noise, probably can't hear some birds beyond 25m

Wind (Beaufort scale):

0 - smoke rises veritically
1 - wind direction shown by smoke drift
2 - wind felt on face, leaves rustle
3 - leaves, small twigs in constant motion, light flag extended
4 - raises dust and loose paper, small branches are moved
5 - small trees with leaves sway, crested wavelets on inland waters

High Tide Time: _______________
Air Temp: _______________

Sky:

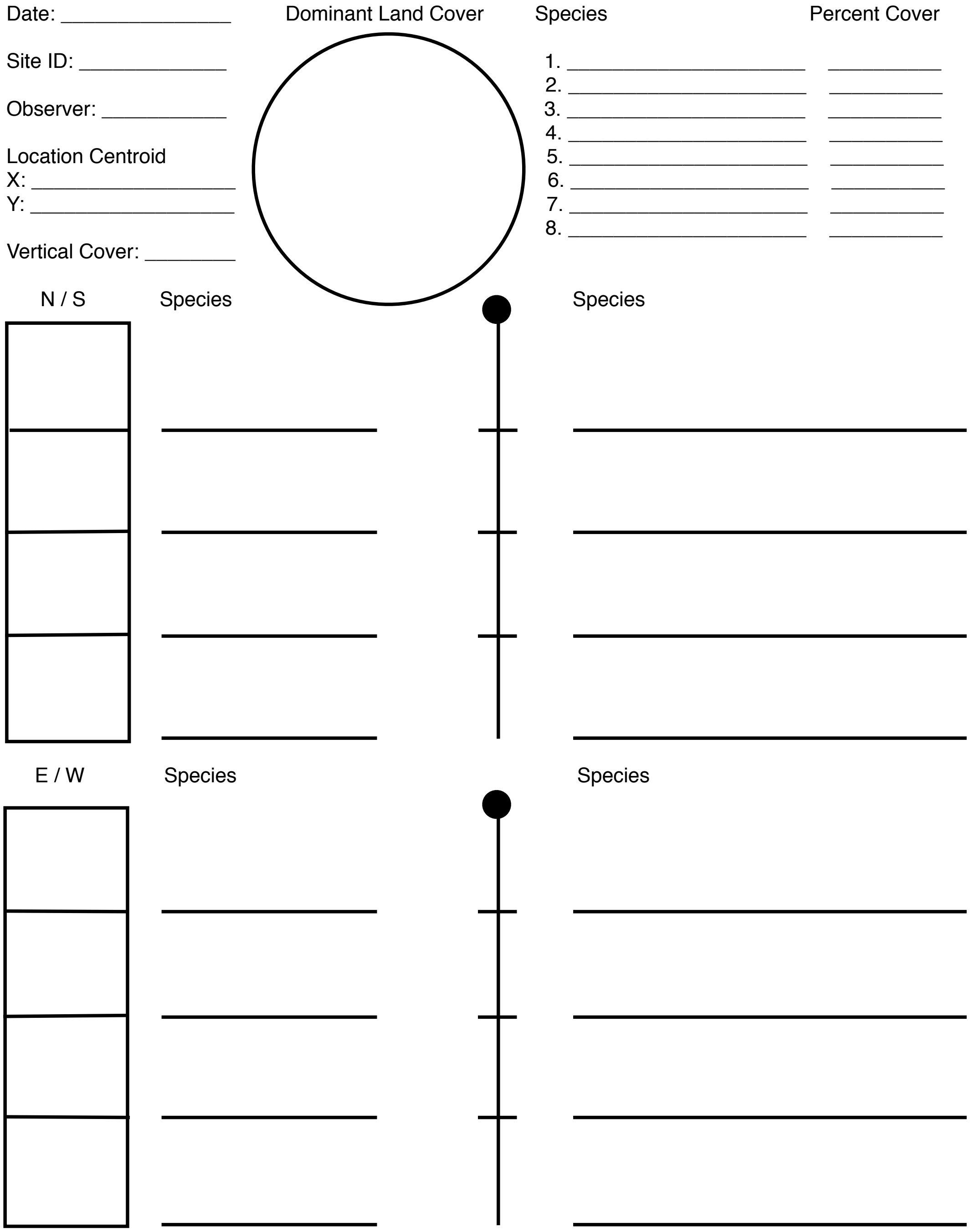
0 - clear or a few clouds
1 - partly cloud or variable sky
2 - cloudy or overcast
4 - fog or smoke
5 - drizzle
6 - snow
8 - showers

Bird Observation Notation

S = Seen
1 = Heard
1S = Seen & Heard

		Responded During															
		Silence					Call-Back										
Start Time	Species	1	2	3	4	5	BLRA	LEBI	VIRA	KIRA	COMO	Outside Survey Period	Call Type(s)	In Target Area	Distance (m)	Detected at a Prev. Point?	Comments

Figure A.1: The data sheet used for call-broadcast surveys.



Date: ________________

Site ID: ______________

Observer: ____________

Location Centroid
X: ___________________
Y: ___________________

Vertical Cover: _________

Dominant Land Cover

	Species	Percent Cover
1.		
2.		
3.		
4.		
5.		
6.		
7.		
8.		

N / S

Species

Species

E / W

Species

Species

Figure A.2: The data sheet used for microhabitat surveys at call-broadcast points and nest locations.

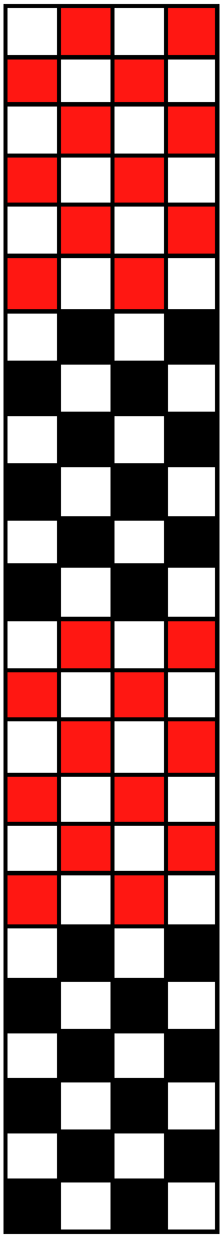
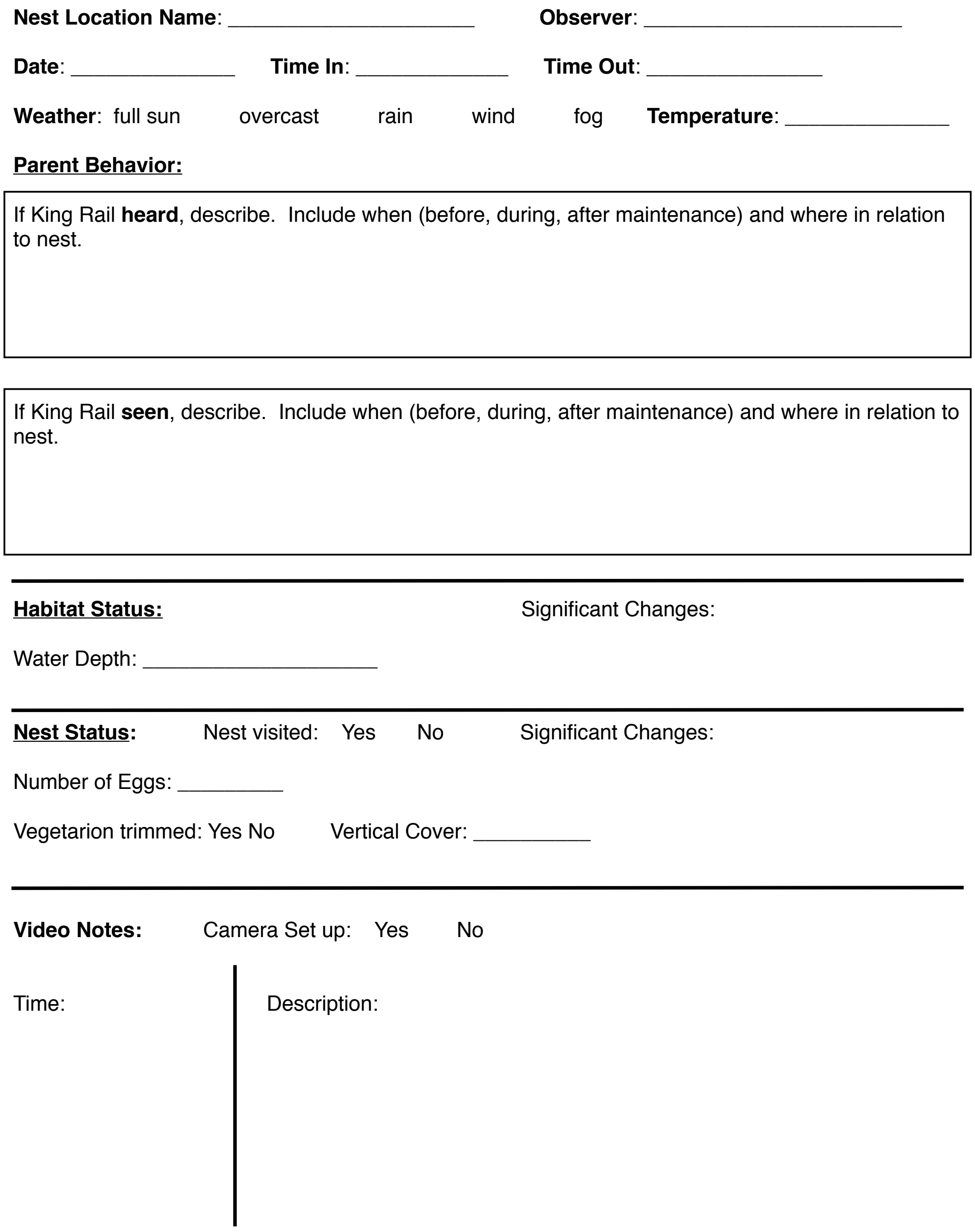


Figure A.3: The density board design used to measure horizontal cover during microhabitat surveys.



Nest Location Name: ______________________ **Observer**: ______________________

Date: ______________ **Time In**: _____________ **Time Out**: _______________

Weather: full sun overcast rain wind fog **Temperature**: ______________

Parent Behavior:

If King Rail **heard**, describe. Include when (before, during, after maintenance) and where in relation to nest.

If King Rail **seen**, describe. Include when (before, during, after maintenance) and where in relation to nest.

Habitat Status: Significant Changes:

Water Depth: ____________________

Nest Status: Nest visited: Yes No Significant Changes:

Number of Eggs: _________

Vegetarion trimmed: Yes No Vertical Cover: __________

Video Notes: Camera Set up: Yes No

Time:	Description:

Figure A.4: The data sheet used for nest visits.

Appendix B

Video Monitoring Set-Up

For nest locations with feasible access, a video monitoring system was set up for the duration of nest activity. The monitoring system was composed of a Q-See CCTV color infrared camera connected to an 8.9-inch Asus Eee PC netbook computer by a Hauppauge WinTV-HVR analog-to-digital data converter. The recording system was powered by two Werker marine cell, deep cycle batteries (12 volts, 33 amp hours). The batteries were connected to the camera and the computer through a customized plug system made using Radioshack Adaptaplug components (Figure B.1). Two available solar panels were also used to power the video systems at the nests farthest away. Video data were recorded onto Centon Datastick Pro 16 GB thumb drives, which could hold a maximum of 60 hours of data. The video systems were visited daily to switch batteries and thumb drives and to check the system status.

Variable field conditions required the systems to be well shaded and waterproofed. The computer and batteries were placed in separate 30 qt. clear plastic storage containers. Wooden shipping palettes fitted with pool noodles provided a floating platform for the containers. A 1.2 m x 1.2 m PVC frame covered with camouflage fabric protected the systems from direct sunlight. The sides were kept open to allow air flow for cooling (Figure B.2).

The QSee camera was mounted on a PVC pole within 1 m above or beside the nest depending on the vegetation structure. The cameras were camouflaged using plastic coke bottles that had been cut in half, painted green and covered with local grasses (Figure B.3). The floating platform was positioned 20 m from the camera to minimize the foot traffic leading to the nest. However, the nest was visited occasionally to trim the vegetation that blocked the camera's line of sight.

Each netbook computer ran CrunchBang Linux 8.10.02 (http://crunchbanglinux.org/), which was chosen for its low resource usage, allowing a greater proportion of the netbook's memory and CPU to be devoted to video processing. The program tvtime (http://tvtime.sourceforge.net/) was used during nest visits to view the camera image in real-time and to test the field of view and data input quality. The nest video was recorded at 4 fps and 500 kbps VBR using mencoder (http://www.mplayerhq.hu). Video data were recorded in an AVI container using the FFmpeg libavcodec (lavc) mpeg4 part 2 encoder. At these settings, a 24-hour video averaged 5-6 GB in size, with larger file sizes occurring on windier days. Data were viewed with VLC Media Player (http://www.videolan.org/vlc/) .

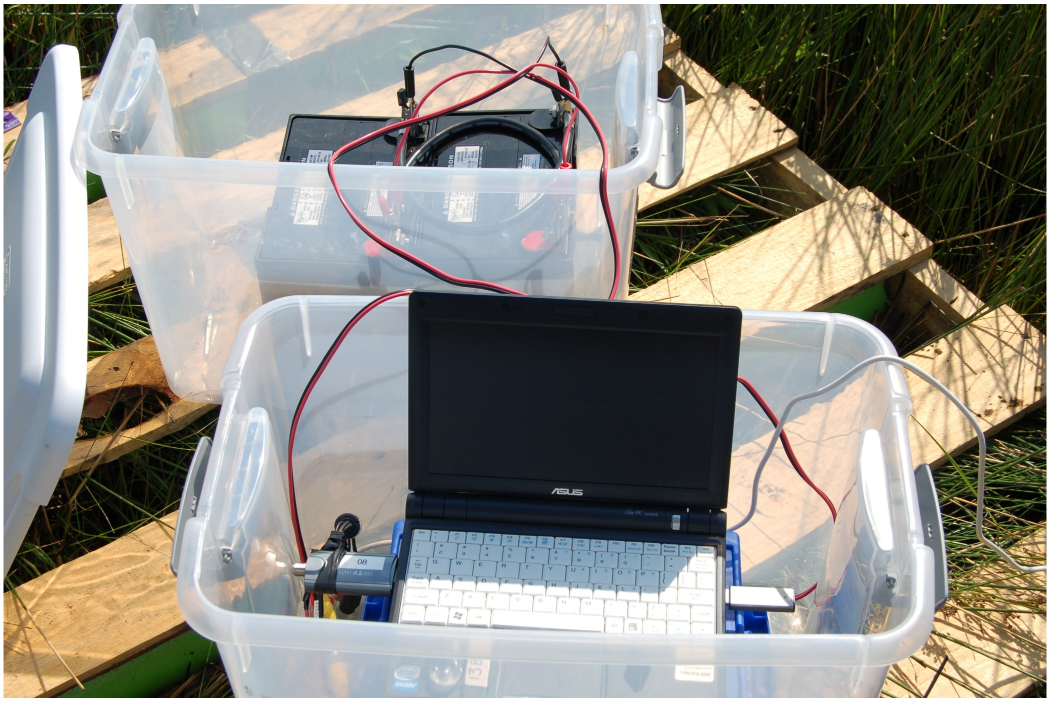


Figure B.1: The video monitoring system used to record nest activity of King Rails. Data were recorded by a netbook computer onto thumb drives. The computer was powered by two marine cell, deep cycle batteries.

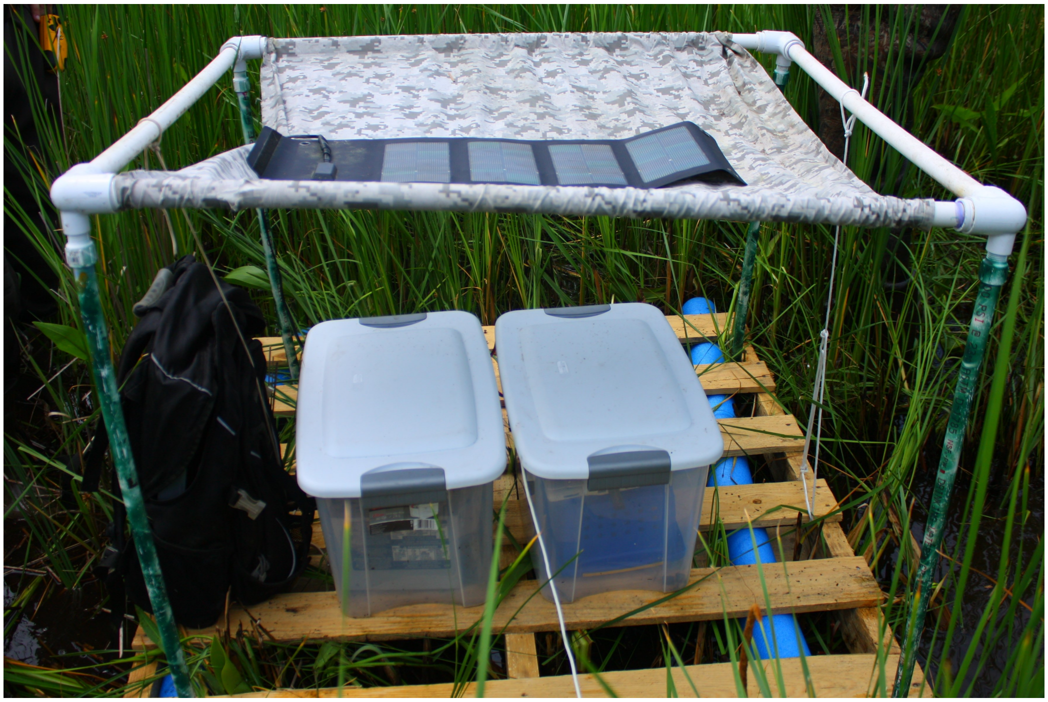


Figure B.2: The video monitoring system used to record nest activity of King Rails. Solar panels were also available to power the systems. The computer and batteries were waterproofed through the use of clear plastic storage containers and a shaded floating platform. The platform was located 20 m from the camera.

Figure B.3: The video monitoring system used to record nest activity of King Rails. The camouflaged camera was placed within 1 m from the nest and connected to the rest of the set up 20 m away.

Appendix C

Nest Predators

Of the fourteen nests documented via video surveillance, five failed due to predation. Predators identified in the video were raccoon (*Procyon lotor*; Figure C.1), black rat snake (*Elaphe obsoleta obsoleta*; Figure C.2), and eastern cottonmouth (*Agkistrodon piscivorus piscivorus*; Figure C.3); however, not all snakes were identified from video footage due to video quality or distance from the camera. Predators visited nests in all nesting stages: egg laying, incubation, post-hatch and abandonment, as well as empty nests. Three of the nests were depredated by a snake during the egg laying period, and two, by a raccoon at the end of the incubation period. In general, predators either ate all or none of the eggs at a nest.

In most cases, the parent King Rail flushed prior to the arrival of a predator. Flushing occurred as little as 4 s before and as much as 27,593 s before a predator arrived. In cases where there were multiple predator visits during a 24-hour period, the parent King Rails do not return in between predator visits. There was only one instance when a predator and a parent were both present at the nest; the eastern cottonmouth and the parent King Rail both left the nest when they saw the other.

For nests located in habitat that had been burned the same year (*i.e.*, 0 years since burn), 88.89% (8 of 9) had at least one documented predator at the nest. For nests located in habitat burned the previous year (*i.e.*, 1 year since burn), 50% (2 of 4) had at least one documented predator. The only monitored nest located in 2 years since burn habitat did not have any documented predators.

There were six raccoon visits at four recorded nests from 2009 and 2010. The earliest visit was recorded at 9:54 PM and the latest at 4:09 AM. The duration of raccoon visits ranged from 14 seconds to 1,184 s with a mean of 300 s and a median of 145 s. Raccoons ate eggs if any were present.

There were twenty-four snake visits at nine recorded nests from 2009 and 2010. At three visits, a nest was terminated; at fifteen, no eggs were eaten; at six, the nest was already empty.

Of all snake visits, eleven were recorded at night and thirteen during the day. Night visits were those that took place when the camera light was turned on. Snakes remained at the nest when eating or trying to eat eggs. The duration of snake visits ranged from 9 s to 3,871 s with a mean of 669 s and a median of 259 s.

Snakes that were identified as eastern cottonmouths were never successful at taking eggs from the nest. This inability to eat King Rail eggs could be due to a gape limitation (Vincent et al. 2004). Measurements of King Rail egg widths/heights from this study (31.03 mm ± 1.403 mm) were greater than the average widths and heights of cottonmouth prey (10.3 mm ± 7.80 mm and 16.4 mm ± 7.40 mm, respectively, for males; Vincent et al. 2004). Multiple visits by eastern cottonmouths within a 24-hour period were documented, and the snake attempts to eat the eggs at each visit, although the subsequent visits were shorter in duration. Eastern cottonmouths were also recorded remaining at the nest, paying more attention to the vegetation surrounding the nest.

Black rat snakes that were identified ate all eggs at the nest, requiring less time to eat each successive egg. After all eggs were eaten, the snake circled the nest, entering from different directions, and used its head to search through the vegetation. Black rat snakes are opportunistic foragers that may be more abundant at habitat edges (Weatherhead et al. 2003) and have been found to eat all contents at a nest (Stake et al. 2005).

A description of predator events for each nest is given below, and a summary is provided in Table C.1.

- 2009_BB01: a black rat snake visited once where five eggs were abandoned after six had previously hatched, but did not eat any eggs.
- 2009_BB02: a snake visited once after six of twelve eggs had hatched, but did not eat any remaining eggs. Three more visits were made by a snake two days later to the empty nest after the last six eggs hatch.
- 2009_MI01: a snake visited once during the egg laying period and ate all three eggs present.
- 2009_MI06: an eastern cottonmouth visited in the middle of the incubation period, but did not eat any of the eleven eggs present. When the snake arrived at the nest, the parent King Rail was sleeping with its head under its wing. The two made eye contact, and both left the nest quickly. The nest was terminated across two visits by a raccoon. The first visit was at 4:09 AM; the raccoon ate nine out of eleven eggs. Both parents returned to the nest after the raccoon left. A raccoon ate the last two eggs during a second visit that evening at 9:55 PM. The raccoon sat outside the nest and reached in to grab eggs one at a time during both visits. The parents did not return to the nest for the remaining day

of video footage. It is hypothesized that the raccoon did not finish the last two eggs at the first visit, because it had previously terminated a nearby Least Bittern nest.

- 2009_MI08: an eastern cottonmouth visited seven times, tried to eat the two abandoned eggs that were present, but physically could not.
- 2009_MI09: a black rat snake ate all four eggs present. The empty nest was revisited three times during the following day. A raccoon also visited the empty nest the following day. It was unclear whether this nest was terminated in the egg laying period or whether the four eggs were abandoned and the outcome was unknown; no parent King Rail was never seen at the nest during the two days of video monitoring.
- 2010_MI01: a black rat snake visited once during the egg laying period and ate all five eggs present. The snake dug through the nest vegetation with its head after all eggs are eaten. The parents did not return to the nest during the two remaining days of video footage.
- 2010_MI02: an eastern cottonmouth visited twice after one egg had hatched, tried to eat the six remaining eggs, but physically could not. The snake spent time at the nest climbing the vegetation as well. The fate of these six eggs was unknown. A raccoon visited the empty nest four days later. The parents did not return to the empty nest in the remaining day of video footage.
- 2010_MI04: an eastern cottonmouth visited three times during one evening, but did not eat the two abandoned eggs present. Each visit was shorter in duration. The snake tried to eat the eggs each time, but physically could not.
- 2010_MI05: a raccoon visited a nest at the end of incubation and ate eight of the nine eggs present. The raccoon sat at the nest, and looked at the camera several times while eating the eggs. The raccoon revisited the nest three hours later and ate the egg it missed. The raccoon then looked at and tried to climb on the camera before destroying the nest and leaving. The parents did not return to the nest in the two remaining days of video footage.

Literature Cited

Stake, M. M., F. R. Thompson, III, J. Faaborg, and D. E. Burhans. 2005. Patterns of snake predation at songbird nests in Missouri and Texas. *Journal of Herpetology* 39(2): 215-222.

Vincent, S. E., A. Herrel, and D. J. Irschick. 2004. Sexual dimorphism in head shape and diet in the cottonmouth snake (*Agkistrodon piscivorus*). *Journal of Zoology, London* 264: 53-59.

Weatherhead, P. J., G. Blouin-Demers and K. M. Cavey. 2003. Seasonal and prey-size dietary patterns of Black Ratsnakes (*Elaphe obsoleta obsoleta*). *American Midland Naturalist* 150: 275-281.

Table C.1: A summary of visits by nest predators for all video monitored King Rail nests in 2009 and 2010 at Mackay Island NWR and Back Bay NWR. "Eggs at nest" refers to the number of eggs present at the first predator visit. "Eggs taken" is the total number of eggs taken across all predation events.

Nest	YSB	Nest Outcome	Documented Predators	Number of Visits	Eggs Taken	Eggs at Nest
2009_BB01	0	Success	Black Rat Snake	1	0	5
2009_BB02	0	Success	snake	4	0	0
2009_MI01	0	Failure	snake	1	3	3
2009_MI06	0	Failure	Eastern Cottonmouth, Raccoon	3	11	11
2009_MI08	0	Success	Eastern Cottonmouth	7	0	2
2009_MI09	0	Unknown	Black Rat Snake, Raccoon	5	4	4
2010_MI01	0	Failure	Black Rat Snake	1	5	5
2010_MI02	0	Success	Raccoon, Eastern Cottonmouth	3	0	6
2010_MI04	1	Success	Eastern Cottonmouth	3	0	2
2010_MI05	1	Failure	Raccoon	2	9	9

Figure C.1: Predation of a King Rail nest by a raccoon.

Figure C.2: Predation of a King Rail nest by a black rat snake.

Figure C.3: Predation of a King Rail nest by an eastern cottonmouth.