MULTI-SCALE ANALYSES OF HABITAT SELECTION AND DEMOGRAPHIC CONSEQUENCES FOR SOUTH CAROLINA CLAPPER RAILS (*RALLUS LONGIROSTRIS*)

by

CATHERINE ELIZABETH RICKETTS

(Under the Direction of Jeffrey Hepinstall-Cymerman)

ABSTRACT

Clapper rails (*Rallus longirostris*) are a secretive gamebird species of coastal tidal marshes. I combined an examination of rail habitat choices at multiple scales with estimation of two demographic parameters, studies of which were until now, non-existent for Atlantic coast populations. I determined the sex of captured rails (n = 82) using genetic testing of tissues to examine potential sex-based differences in habitat choices or survival. I radio-tracked 83 rails during the 2009 and 2010 breeding seasons and found that rails selected home ranges with more foraging area than available across the landscape which possibly increased survival. Rails selected nest sites with lower tidal maxima than available across the landscape, in part, resulting in higher nest survival (i.e., a successful hatching event). It is evident that a year-round radio-tracking effort and explicit studies of the distribution and densities of clapper rail prey items would answer questions emerging from this work.

INDEX WORDS: clapper rail, home range selection, nest site selection, survival, nest success

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DEDICATION

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

INTRODUCTION AND LITERATURE REVIEW

Across the United States more than 1.2 million hectares of wetlands were converted for human uses between the mid–1970's and 1997 (Dahl and Johnson 1991, Dahl 2000, Dahl 2006, Cooper 2007). Mitigation and restoration efforts between 1998 and 2004 resulted in an overall increase in wetland area, but total hectares of tidal marsh, both freshwater and brackish, declined slightly during that same time period (Dahl 2006). The quality of remaining natural tidal marsh habitats is affected by invasive plants, fragmentation, pollution, siltation, dredging, and channelization (Cooper 2007, Cumbee et al. 2008). Moreover, it is unclear if anthropogenic wetlands, including marshes, are capable of sustaining marsh obligate species such as king rails (*Rallus elegans*) and clapper rails (*R. longirostris*) (Boyer and Zedler 1998, Melvin and Webb 1998, Desrochers et al. 2008).

Scattered along the South Atlantic Coast of the U.S. are thousands of hectares of existing coastal wetland impoundments. For example, an estimated 54,500 ha (27%) of South Carolina's 204,000 ha of coastal tidal marsh are functioning or remnant wetland impoundments (Gordon et al. 1989). These impoundments are interspersed within the gradient of natural freshwater, brackish, and salt marshes. Coastal impoundments in the southern U.S. originated from pre-Revolutionary War economic enterprise. Rice farming began in forested wetlands near the coast, but reliance on unpredictable precipitation for irrigation limited production. Farmers soon recognized the advantages of tidal fluctuations in providing consistent water for their crops. Using slave labor, coastal impoundments were built with unique water control structures called ricefield trunks. These trunks connected impounded areas with tidal rivers. By adjusting gates on one or both sides of the impoundment and adding or removing riser boards, farmers manipulated both water and salinity levels. Despite great prosperity during the late 1700s through the mid 1800s, the rice industry of the South Atlantic declined after the Civil War. Tropical storms damaged farming operations and slave labor was no longer available, making rebuilding a financial impossibility (Gordon et al. 1989).

As the 1900s began, the role of southern coastal impoundments shifted from agriculture to wildlife management. Northern industrialists discovered the tracts of riverfront property encompassing old rice plantations and purchased these as hunting retreats. They maintained the structural integrity of impounded areas to attract waterfowl which they hunted during fall and winter. The most recent estimate finds approximately 28,500 ha of intact impoundments currently under management in South Carolina (Gordon et al. 1989). These areas have supplemented natural tidal marsh habitat for migrating and wintering waterfowl across a range of salinity values (Prevost 1987).

Resource managers in the South recognized the potential of these impoundments to provide habitat for species in addition to waterfowl (Strange 1987). Prior research in coastal locations (e.g., New Jersey, South Carolina, Delaware, and Louisiana) has focused on integrating management for migrating shorebirds into areas already managed for waterfowl (Erwin et al. 1994, Weber and Haig 1996, Huner et al. 2002, Parsons 2002), but relatively few studies have investigated methods to include locally breeding marsh birds (Post 1998, McGregor 2007). Work conducted at interior wetlands in Iowa, California, and New York suggests that impoundments could increase available habitat for marsh birds while not detracting from the benefits to waterfowl (Johnson and Dinsmore 1986, Taft et al. 2002, Lor and Malecki 2006). Two marsh birds that could benefit from supplemental habitat provided by southern coastal impoundments are the king rail (*Rallus elegans*) and the clapper rail (*Rallus longirostris*).

Population issues

In the United States clapper rail habitat is delineated by the extent of brackish water in coastal marshes (Meanley 1985). The Atlantic Coast is home to three of eight U.S. subspecies of clapper rails. *R. l. crepitans* breeds in marshes from Massachusetts to southern Virginia and may travel to the South Atlantic marshes for the winter (Eddleman and Conway 1994). *R. l. waynei* ranges from northern North Carolina to northern Florida and is not believed to migrate (Eddleman and Conway 1994). The range of *R. l. scotti* is entirely within Florida (Eddleman and Conway 1994).

Clapper rail populations are believed to be stable along the Atlantic coast although habitat loss and degradation is an ongoing concern (Eddleman and Conway 1998). Many clapper rails do not migrate or migrate only short distances (Hon 1972, Mangold 1974, Crawford et al. 1983, Eddleman and Conway 1994). Residents may be more vulnerable to habitat degradation particularly if this degradation is not easily detected by the birds (Greenberg et al. 2006a). For example, chemicals from contaminated marsh ecosystems can cause death or deformities in young rails and embryos (Springer and Webster 1951, Schwarzbach et al. 2006) and can accumulate in adult birds (Van Velzen and Kreitzer 1975, Cumbee et al. 2008).

General habitat for king rails is freshwater marshes of the eastern U.S. and southern portions of Eastern Canada (Meanley 1969). There is a single subspecies of king rail (*R. e. elegans*) in continental North America. Birds from the northern part of the range (e.g., upper Midwest, New

England) are believed to migrate to the Gulf and Atlantic Coasts via the Mississippi and Atlantic Flyways (Meanley 1969, Poole et al. 2005).

Current king rail population trends show a significant decline since 1966 (MSUGBSTF 2009). Habitat loss is cited as one of the main threats to this species (Poole et al. 2005). Shrinking population numbers are more severe in the northern part of the king rail range and in Canada it is federally endangered (COSEWIC 2000). The U.S. Fish & Wildlife Service (USFWS) has categorized it a “Bird of Management Concern,” a “Gamebird Below Desired Condition,” and a focal species within its “Focal Species Strategy for Migratory Birds” (Cooper 2007). States have also recognized the decline in king rail numbers: 29 consider the king rail a “Species of Greatest Conservation Need” and 12 have listed the bird as Threatened or Endangered (Cooper 2007).

Officially king and clapper rails remain classified as two separate species (American Ornithologists’ Union 1983), but there is some debate as to whether king and clapper rails are members of the same species (Avise and Zink 1988, Chan et al. 2006). King and clapper rails can hybridize (Meanley and Wetherbee 1962) although in coastal tidal marshes these two rail species typically segregate along a salinity gradient. Clapper rails have not been observed in freshwater marshes but there have been king rail sightings in brackish marshes (Meanley and Wetherbee 1962, Meanley 1969, Olson 1997). Salinity was identified recently as a significant factor in explaining observed genetic variation between king and clapper rails (Maley and Brumfield 2010). Other DNA evidence supporting the distinction between these two rails is equivocal, implying a recent divergence in the lineage (Avise and Zink 1988, Chan et al. 2006). Common morphometric measurements may overlap between the species (Perkins et al. 2009) but internal skeletal structures, in particular the interorbital bridge, show evidence of distinct heritable differences (Olson 1997): the width of the interorbital bridge in clapper rails was found to be thinner to accommodate a larger nasal salt gland than the width in king rails (Olson 1997).

Clapper and king rails also exhibit some of the differences in survival and reproductive strategies documented for tidal marsh birds and their non-tidal marsh relatives. The duller, gray-brown feathers of clapper rails (compared to the rustier feathers of the king rail) are consistent with coloration of other tidal marsh obligate species as an adaptation to avoid predation while foraging on open mudflats (Greenberg and Droege 1990). Clutch sizes for clapper rails are smaller than for king rails (Meanley 1969, Meanley 1985). A similar pattern is described as a response by tidal marsh sparrow species to increased nest predation risk in coastal environments (Greenberg 2006b).

Both rail species are gamebirds but neither is hunted intensively today (Eddleman and Conway 1998, Poole 2005). In the entire Atlantic Flyway, harvest of clapper rails was estimated at 8,600 birds in 2006 and 10,000 birds in 2007 whereas king rail harvest was estimated at < 50 birds each year (Richkus et al. 2008). These numbers are low compared to harvest numbers for other migratory gamebirds, but the daily bag limit for both species in many states is between 10 to 15 birds (Eddleman and Conway 1998, SC DNR 2008). Harvest data for rails lack spatial resolution and are aggregated to the state level. For example, preliminary harvest estimates of all rail species—Virginia rail (*R. limicola*), clapper, king, and sora (*Porzana carolina*)—taken in South Carolina report 3,600 ± 117% during the 2006 season and 2,400 ± 127% during the 2007 season (Richkus et al. 2008).

Research needs

Uncertainty exists not only in harvest estimates, but also in long–term population trends for both king and clapper rails. In fact, there is no current estimate of population size for either species at a national or flyway level (MSUGBSTF 2009). Traditional survey methods (e.g., Breeding Bird Survey and Christmas Bird Count) are inadequate for secretive marsh species including rails because of poor human accessibility to tidal marshes resulting in low spatial coverage of the habitat (Gibbs and Melvin 1993, Conway and Gibbs 2005). Low detection rates with high variability (e.g., observed coefficient of variation of 189%) compound the inadequate sampling coverage, further reducing precision in population modeling efforts (Gibbs and Melvin 1993, Conway and Gibbs 2005). New monitoring techniques have been developed (Conway 2008), but robust historical data are lacking (Cooper 2007). A recent workshop convened by the Association of Fish and Wildlife Agencies' Migratory Shore and Upland Game Bird Support Task Force prioritized the information needed to reduce these uncertainties. The highest priority is to implement a national monitoring program followed by improvements to the Harvest Information Program and parts collection survey. The final priority is to estimate vital rates to support population modeling (MSUGBSTF 2009).

A local population's vital rates reflect each member's individual fitness. An individual's fitness is linked to its habitat (Fretwell and Lucas 1970). If the relationships among habitat characteristics and survival and reproductive outcomes for a species are not investigated, resulting management actions can be ineffective, wasting resources and conservation opportunities. For king and clapper rails these connections are now being emphasized in current research (e.g., Rush et al 2010c, Rogers 2011).

Previous studies described the natural history of Atlantic Coast clapper and king rails, including general habitat associations, basic breeding biology, and nest characteristics (Stewart 1951, Oney 1954, Adams and Quay 1958, Blandin 1963, Meanley 1969, Mangold 1974, Meanley 1985, Gaines et al. 2003, McGregor 2007). Research has documented rail presence or densities and recorded habitat metrics, but neither reproductive success nor adult survival data (if any) were formally associated with habitat data through statistical analyses or experimentation. In the 1950s through the early 1970s, eastern clapper rail research foci were to develop population indices and to gather movement patterns to better inform sportsmen of the birds as a hunting opportunity (Stewart 1951, Hon et al. 1972, Mangold 1974). Thus, estimates both of population numbers and of basic demographic parameters are non–existent. Although the data collected are insufficient to quantify retroactively the relationships among habitat characteristics, reproductive outcomes, and survival, the information is useful to formulate hypotheses for studies that will address these relationships. A growing body of recently published work, especially on Gulf Coast rails, is available for comparison (Darrah and Krementz 2009, Rush et al. 2010a, Rush et al. 2010b, Rush et al. 2010c)

Habitat associations

Smooth cordgrass (*Spartina alterniflora*), big cordgrass (*Spartina cynosuroides*), saltmarsh bulrush (*Schoenoplectus robustus*), and black needlerush (*Juncus roemerianus*) typify vegetation of the South Atlantic Coast brackish marshes where clapper rails occur (Adams and Quay 1958, Lewis and Garrison 1983, Meanley 1985, Eddleman and Conway 1994, McGregor 2007). In marshes dominated by *Spartina* spp., vegetation height (vertical structure) and stem density tend to decrease with increasing distance from tidally influenced rivers and creeks (Lewis and Garrison 1983). Oney (1954) classified "tall forms" of smooth cordgrass as adjacent to these tidal rivers and creeks and up to1.2 m to 2.4 m tall; "medium forms" are between 0.6 m and 1.2 m tall; and "short forms" are < 0.6 m. Clapper rail presence is associated with the tall and medium forms of smooth cordgrass more than the short forms during the breeding season (Stewart 1951, Oney 1954, McGregor 2007). The light-footed clapper rail (*R. l. levipes*) avoided a constructed *Spartina* spp. marsh system in California because vegetation height was too short (Boyer and Zedler 1998). Surveys of rails in the fall and winter are sparse but indicate that rails occupy habitat with vegetation of a height similar to the vegetation heights in their summer habitats (Lewis and Garrison 1983, McGregor 2007).

Distance to a tidal river or creek and water depth can indicate clapper rail presence (Lewis and Garrison 1983). Together these measurements may relate to food availability. Fiddler crabs (*Uca* spp., *Sesarma* spp.) are one of the most important prey items for rails (Oney 1951, Lewis and Garrison 1983, Meanley 1985, Rush et al. 2010b). During low tide periods, clapper rails move closer to the exposed banks of a tidal waterbody to forage for crabs and other prey (Meanley 1985, Rush et al. 2010a). A habitat suitability index (HSI) described the most suitable rail habitat to be within 15 m of water's edge (Lewis and Garrison 1983). High interspersion of vegetation and water (i.e., edge) has been found to indicate presence of other secretive marsh species, e.g., Virginia rail, sora, and least bittern (*Ixobrychus exilis*) (Rehm and Baldassarre 2007), and may also apply to clapper rail presence.

Atlantic Coast clapper rail nest sites are associated with the interface between tall and medium forms of smooth cordgrass and closer proximity to a tidal river or creek (Stewart 1951, Lewis and Garrison 1983, Meanley 1985). Along the Georgia coast, vegetation height at nest sites ranged from 0.6 m–1.22 m (Lewis and Garrison 1983, Gaines 2003) and nests were within 8 m of a water source (Gaines 2003). In New Jersey, a majority of nests were in smooth cordgrass at least 0.61 m tall and within 3.65 m of water (Kozicky and Schmidt 1949). Taller vegetation is believed to reduce predation risk by providing increased overhead cover and to protect from tidal flooding because nests can be constructed above the high water line (Adams and Quay 1958, Meanley 1985, Storey et al. 1988, Gaines 2003). In Mississippi, rails selected nest sites with greater stem densities and taller vegetation than control sites (Rush et al. 2010c).

King rails inhabit a wide variety of wetland habitats throughout their range (Meanley 1969, Poole et al. 2005) but along the Atlantic Coast they are often found in freshwater and brackish marshes composed of saltmeadow cordgrass (*Spartina patens*), smooth cordgrass, Olney's three–square (*Shoenoplectus americanus*), saltmarsh bulrush, big cordgrass, and marsh elder (*Iva fructens*) (Meanley and Wetherbee 1962, Meanley 1969). In South Carolina, a combined assessment of king and clapper rails found their presence was associated with a mean marsh vegetation height of 1.54 m ± 0.89 m in the summer and 1.73 m ± 0.13 m in winter (McGregor 2007). In Missouri, mean vegetation height of king rail habitat was 0.51 m ± 0.018 m during spring, and 0.78 m ± 0.067 m in fall (Reid 1989). Stem density was 293 stems/m^2 ± 29 stems/m^2 in spring and 308 stems/m^2 ± 36 stems/m^2 in fall (Reid 1989). Another study found neither tall nor short emergent vegetation indicated king rail site occupancy (Darrah and Krementz 2009); instead king rail occupancy corresponded positively with high interspersion of vegetation and water (Darrah and Krementz 2009).

King rails also forage on shallowly flooded or exposed mudflats for preferred prey items such as fiddler crabs, crayfish, and other invertebrates (Meanley 1969, Poole et al. 2005), but whether distance to water's edge is a useful indicator of king rail presence is unknown. In Georgia, king rails were associated with water depths of 2–5 cm during breeding season (Meanley 1969). Another study reported a mean breeding season water depth of 29 cm ± 7.6 cm recorded at point count survey stations associated with both king and clapper rail presence (McGregor 2007).

Few details are available on king rail nests sites along the Atlantic Coast. Two king rail nests were found approximately 0.6 m above the low–tide mark in South Carolina but vegetation height was unknown (Meanley 1969). A group of nests were located within 6 m of a marsh edge near Savannah, Georgia (Meanley 1969).

Several studies attempted to quantify the amount of habitat individual rails require. Territorial behavior during breeding season has been observed in both species (Meanley 1969, Lewis and Garrison 1983) and intraspecific competition likely impacts rail densities and home range sizes and placement in a particular habitat. In Georgia, clapper rail breeding density was 2.2 to 3.7 birds per hectare and clapper rail fall density was 3.2 birds per hectare (Oney 1954). In another study, mean breeding season home range size using 100% Minimum Convex Polygon (MCP) was 1.2 ha (range for 4 females: 0.17 ha to 0.77 ha; range for 3 males: 0.27 ha to13.3 ha) (Cumbee et al. 2008). In coastal South Carolina, breeding season MCP home ranges for two clapper rails were 7.3 ha and 0.4 ha (McGregor 2007). In North Carolina, one study found clapper rails shifted their home ranges from smooth cordgrass and black needlerush dominated low marsh in summer to saltmeadow cordgrass high marsh in winter (Adams and Quay 1958).

On the South Atlantic Coast king rail breeding season densities were 1.2 birds per ha and 5.3 birds per ha; in Maryland, 2 birds per ha (Meanley 1969). A breeding season MCP home range for a single bird in South Carolina was 90.5 ha (McGregor 2007).

STUDY OVERVIEW

A common research objective in developing management strategies is to identify “high quality habitat”—where populations persist and growth rate is positive—for a particular species. In this context, habitats historically were labeled high quality if they were deemed to include sufficient resources for the species under investigation, but without verification of population parameters (Van Horne 1983). Currently, researchers usually assess habitat quality using demographic metrics because of the inherent relationships among an individual's fitness, its habitat, and population level consequences (Fretwell and Lucas 1970, Johnson 2007). Studies of an individual's condition or of habitat selection are other methods to distinguish high and low quality habitats. Combining more than one method provides greater insights into the system in question (Johnson 2007).

In this thesis, I report on a study that continued and extended a pilot study which gathered habitat and movement data for king and clapper rails in South Carolina's managed (i.e., impounded) and unmanaged (i.e., broken-dike impoundments and tidal marsh) wetlands (McGregor 2007). The goal of my study was to synthesize habitat and demographic parameters for both rail species to describe characteristics of quality habitat during winter and breeding seasons. This information addressed, in part, concerns for these rails set forth by the Migratory Shore and Upland Game Bird Support Task Force, the Webless Migratory Game Bird Research Program, the South Atlantic Migratory Bird Initiative, and the South Carolina State Comprehensive Wildlife Conservation Plan. In collecting data to satisfy the above goal, the potential for coastal wetland impoundments to supplement natural rail habitat was examined. Given the paucity of data on rail demographics and what constitutes high quality rail habitat, this study supplies needed information for researchers and resource managers.

This project was originally envisioned as a comparative study between king and clapper rails for the results of each objective below. However I did not capture enough king rails to allow this type of analysis between species. Appendix A provides the information collected on king rails. As such, the following objectives focus on clapper rails only.

STUDY OBJECTIVES

In Chapter 2, I discuss objective one: identify the sex of rails captured during this project. Clapper rails show within-species sexual plumage monomorphism (Meanley 1985). This species shows sexual size dimorphism but sex differentiation is not evident from visual or behavioral (e.g., both sexes incubate a nest) observation in the field. A recent Louisiana study found that a combination of morphometric measurements could accurately predict rail sex, but questioned the ability to use this calculation across geographic regions (Perkins et al. 2009). I used genetic testing from DNA collected from feather and blood samples to determine the sex of each rail. In addition, I used the genetic results to test the ability of morphometric measurements to identify rail sex for both the Atlantic and Gulf populations.

In Chapter 3, I cover the second objective of this project which was to investigate winter and breeding season habitat selection at the home range scale, home range size, and survival of adult clapper rails within brackish tidal marshes of coastal South Carolina. In the pilot study, data collected from radio–telemetry on rail distributions were sparse due to low trapping success (clapper rails: n = 5) and a 73% loss of tagged rails during the study (McGregor 2007). I employed a new trapping technique (Mills et al. 2011) to augment rail sample sizes. I recorded locations of radio–marked clapper rails during 2009 and 2010 to document seasonal use of managed impoundments and tidal marsh. I collected local-scale vegetation and distance-to-edge measurements in the field and calculated landscape-scale metrics for amount of and distance to foraging areas from geospatial data. I expected that clapper rail home range sizes would be similar between sexes in each season. I also expected that clapper rail home ranges would encompass mainly brackish tidal marsh and would not include use of managed impoundments. I predicted that mortality would be similar both between sexes and during both seasons (study period does not overlap rail hunting season).

In Chapter 4, I cover the third objective of this project which was to describe the relationship between nest site selection and nest success at the landscape and local scales. I collected local-scale vegetation and distance-to-edge measurements in the field and calculated landscape-scale metrics for tidal height and the effective distance to sources of terrestrial predators from geospatial data. I expected that clapper rail nests would be more likely to fail from tidal inundation than predation. I further expected that the cause of failure for nests closer to tidal waterbodies would be tidal flooding while the cause of failure for nests farther from tidal waterbodies would be depredation.

In Chapter 5, I summarize the conclusions from work on each objective, discuss the potential for managed impoundments to supplement rail habitat, and indicate pertinent topics for further study.

STUDY AREA

The Ashepoo-Combahee-Edisto (ACE) Basin in southern coastal South Carolina is largely rural (Coastal Services Center 2000) and provides opportunities to conserve and restore critical habitat for marsh bird species (Tufford 2005). Part of the Basin is within the National Oceanic and Atmospheric Administration's National Estuarine Research Reserve System and contains land protected through the cooperation of State, Federal, private, and nonprofit interests (Coastal Services Center 2000), including the Ernest F. Hollings ACE Basin National Wildlife Refuge (NWR) and Nemours Plantation Wildlife Foundation. Nemours Plantation (3,986 ha) is a privately operated non–profit foundation with a focus on education, research, land stewardship, and restoration of wildlife populations. The relatively undeveloped nature of the ACE Basin and commitment to conservation by numerous organizations provide an ideal study area to investigate habitat requirements of king and clapper rails within a network of managed impoundments and tidal marshes.

My study focused on the Combahee River within the ACE Basin (Figure 1.1). Both Nemours Wildlife Foundation and the Combahee Unit of Hollings ACE Basin NWR are located on this river. The Combahee River Bridge on U.S. highway 17 delineates the legal transition from salt to fresh water. The Combahee Fields and Bonny Hall Units of the ACE Basin NWR are upstream from this bridge and encompass mainly freshwater to slightly brackish tidal marsh and impoundments. Nemours' boundaries are to the north and south of the bridge and marshes range from fresh to brackish. Thus, rails were captured across a gradient of salinity and marsh habitat types. The Combahee Fields Unit has 1,063 ha of impounded wetlands and 112 ha of tidal marsh (McGregror 2007). The Bonny Hall Unit has 688 ha of impounded wetlands (Nareff 2009). Nemours has 124 ha of brackish and freshwater marsh combined, plus 748 ha of former ricefield impoundments (Nareff 2009).

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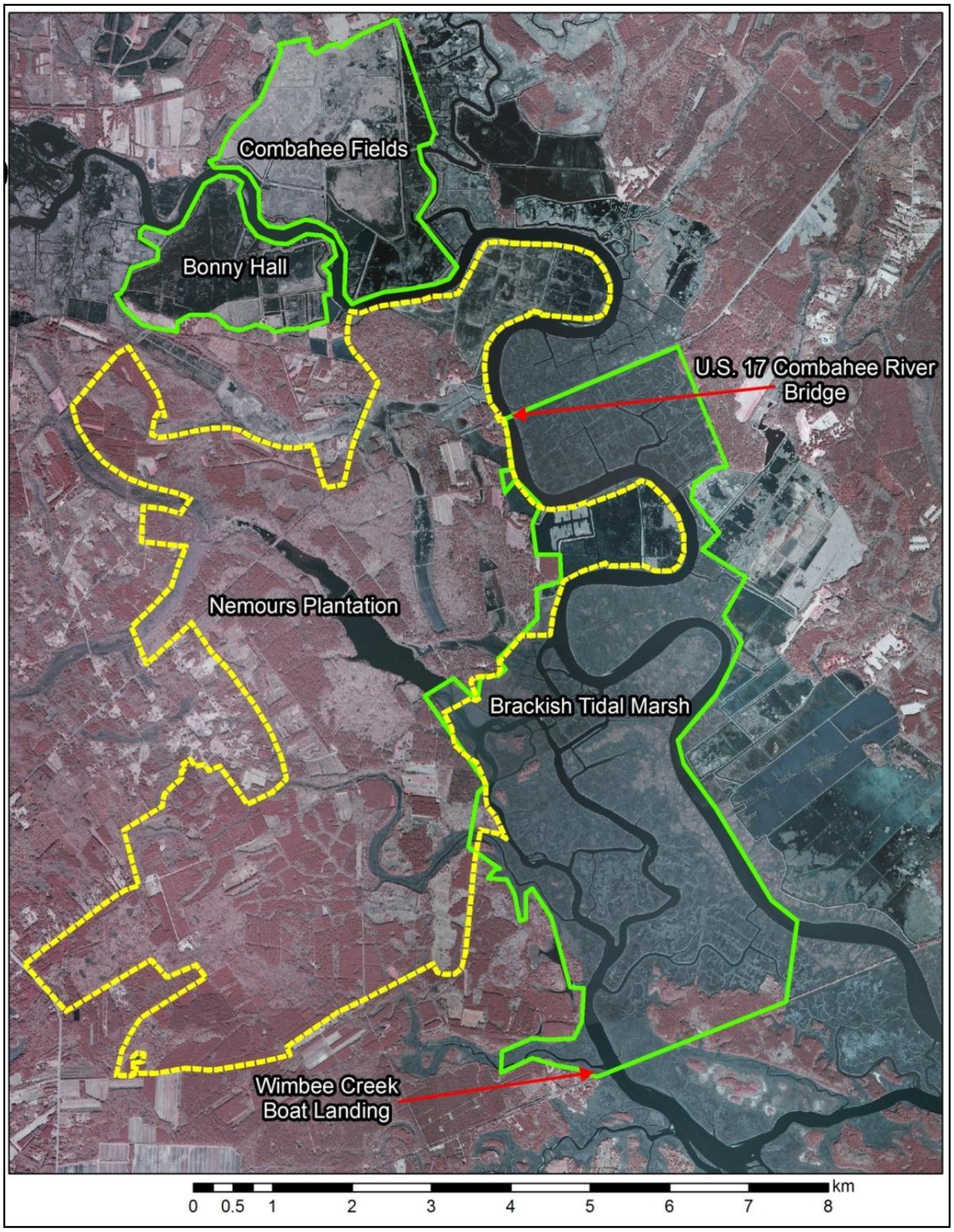

Figure 1.1. Map of clapper and king rail study area sites showing brackish tidal marsh abutting Nemours Plantation where clapper rails were the focus. Bonny Hall and Combahee Fields are two units of the ACE Basin NWR north of the U.S. 17 Combahee River Bridge (denotes the legal transition from salt to fresh water) where king rails were the focus. The Wimbee Creek Boat Landing is the southernmost extent of the study area.

CHAPTER 2

GENETIC AND MORPHOMETRIC DIFFERENTIATION OF SEX IN SOUTH ATLANTIC COAST CLAPPER RAILS (*RALLUS LONGIROSTRIS WAYNEI*)[1]

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[1] Ricketts, C. E., B. C. Shock, M. J. Yabsley, J. Hepinstall-Cymerman, W. E. Mills, and E. P. Wiggers. To be submitted to *Waterbirds*

ABSTRACT

Identifying the sex of living birds exhibiting sexual plumage monomorphism and subtle sexual size dimorphism is important for gaining insight into a species' life history, behavior, and population dynamics. Sex is often determined through genetic testing of tissues such as blood and feathers; however, a field method is preferable. The clapper rail (*Rallus longirostris*) is sexually size dimorphic but differences between males and females are small and size overlap occurs. Work along the Gulf Coast described a discriminant function including wing chord, exposed culmen, and tarsus measurements that was moderately successful in identifying sexes of the resident clapper rail subspecies (*R. l. saturatus*). We developed a logistic regression model from 82 genetically sexed clapper rails (*R. l. waynei*) in South Carolina and found that wing chord and culmen best classified sex (81.5% overall accuracy). We tested our model using the data from the Gulf Coast study to assess its region-wide applicability. Our model had an overall accuracy of 82.6% when predicting Gulf Coast rail sex, suggesting that a region-wide model has some utility.

Key words: clapper rail, morphometric measurements, logistic regression, genetic sexing

INTRODUCTION

The ability to differentiate between male and female birds is important to address questions in topics of avian life history, behavior, habitat selection, and population dynamics. In the field, sexual plumage dimorphism makes this task relatively simple and unambiguous for many species, especially once the birds have molted out of juvenal plumage. Other species, such as the clapper rail (*Rallus longirostris*), do not show sexual plumage dimorphism but show size dimorphism where body measurements for the male are generally larger than for the female (Meanley 1969, Meanley 1985, Eddleman and Conway 1998, Poole et al. 2005) but differences can be subtle (i.e., on the order of mm). Moreover, size overlap does exist between males and females of this species and behavioral cues are ambiguous (e.g., both sexes incubate) so field identification of sex remains difficult.

In earlier studies where the sex of the clapper rail was of interest to the researcher, individual birds were sacrificed or the information was gathered from hunter-killed returns (Meanley and Wetherbee 1962, Mangold 1974, Meanley 1985, Cumbee et al. 2008). Internal examination then provided a definitive answer but with the obvious limitation of no longer being able to observe the bird in the field. Cloacal exam of living birds can only identify after-hatch-year females between February and May (Pyle 1997). Genetic testing of tissues (e.g., feather calamus, blood) is successful and reliable (Griffiths et al. 1998) but represents an added expense in money and time. A field method to reliably determine the sex of living adult clapper rails would be beneficial.

Research has indicated the possibility of using different body measurements to sex clapper rails, but these studies only examined dead rails. A New Jersey study reported that clapper rails (subspecies *R. l. crepitans*) (n = 65) with exposed culmen length ≥ 63.5 mm, longest toe length (including claw) ≥ 63.5 mm, and culmen depth (at distal end of nostril groove) ≥ 7.14 mm were "invariably male" (Mangold 1974). If all measurements were less than that the bird was "invariably female" (Mangold 1974). However, there are no reports of this combination's success either at indicating sex on living birds or indicating sex for a bird with all measurements not above or below the stated thresholds. A Gulf Coast study during hunting season suggested that a rail with mass > 290 g would be male (in Meanley 1985). However, a cut-off value for mass measurements would be unreliable across the clapper rail's range, among seasons, and for females during the breeding season (i.e., gravid vs. non-gravid).

A recent study from the Gulf Coast used multivariate analyses of morphometric measurements to assess which measurements best differentiated between male and female clapper rails (Perkins et al. 2009). Genetic testing was used to conclusively determine sex and measurements for wing chord, tarsus, and exposed culmen were found to be the best predictors. However, Perkins et al. (2009) cautioned against the use of their results for other subspecies of clapper rails found in different geographic regions. The Gulf Coast subspecies is *R. l. saturatus*; the South Atlantic Coast subspecies is *R. l. wanyei*.

The objectives of this study were 1) to identify the sex using analysis of genetic material for each South Atlantic Coast clapper rail caught, 2) to determine which morphometric measurement(s) were the best predictors of rail sex and assess if this method was a viable field alternative to genetic sex differentiation, and 3) to compare these results to the Gulf Coast study to determine if one combination of measurements applies across geographic regions.

STUDY AREA

In this study I focused on an approximately 2,300 ha portion of tidal marsh along the Combahee River and Wimbee Creek within the Ashepoo-Combahee-Edisto (ACE) Basin in southern coastal South Carolina. The study area was approximately 8 km north to south and covered a range of salinity values (W. E. Mills, personal communication). The Combahee River Bridge on U.S. highway 17 delineates the legal transition from salt to fresh water and the highway formed the northern boundary of the study area. The Wimbee Creek Landing was the southern boundary. The western boundary abutted the marsh edge primarily along the Nemours Plantation Wildlife Foundation property line while other private plantation property lines adjacent to the Combahee River formed the eastern boundary.

Smooth cordgrass (*Spartina alterniflora*) dominates the marsh of these two connected water bodies. Black needlerush (*Juncus roemerianus*) grows in largely homogeneous patches mainly in the northern portion of the study area and also in higher elevations throughout. Saltmarsh bulrush (*Schoenoplectus robustus*), big cordgrass (*Spartina cynosuroides*), and soft-stemmed bulrush (*Schoenoplectus tabernaemontani*) are interspersed with smooth cordgrass, mainly in the northern portion of the study area while saltmarsh aster (*Symphyotrichum tenuifolium*) is interspersed with smooth cordgrass throughout the study area (personal observation).

METHODS

In 2009 and 2010 I caught clapper rails from an airboat during high tides using methods described in Chapter 3 and in Mills et al. (2011). In addition, in 2010 I caught two rails off active nests by approaching quietly with dip nets and flushing the bird off the nest into the waiting nets. For all rails, I measured mass (g), exposed culmen (mm), right tarsus (mm), tail (mm), right wing chord (unflattened) (mm), and right middle toe excluding claw (mm). I pulled the 7th primary from the right wing and several outer rectrices which were then stored frozen until genetic analysis. In 2010, I collected a blood sample (≤ 1 mL) using non-heparinized capillary tubes from each bird via venipuncture of the brachial vein. Blood was immediately cooled. Within 2 days blood was centrifuged, plasma was separated from the red blood cells, and both samples were frozen until genetic analysis.

Rail sexing using PCR

I submitted all tissue samples to B. Shock and Dr. M. Yabsley at the Southeastern Cooperative Wildlife Disease Study in Athens, Georgia, who conducted the genetic analyses using the following methodology.

Genomic DNA was extracted from 10 μl of whole blood or approximately 10 mg of feather calamus using the Qiagen DNA Purification Kit (Germantown, MD) following the manufacturer's protocol. A primary PCR protocol that amplifies a ~218 bp region of the W gene (Shizuka and Lyon 2008) was used to detect female rails. For amplification, 5 μl of DNA was added to 20 μl of a master mix containing 10 mM Tris-Cl (pH 8.3), 50 mM KCl, 1.5 mM $MgCl_2$, 0.2 mM each dNTP (Promega, Madison, Wisconsin), 2.5 units Taq DNA Polymerase (Promega), and 0.8 μM of primers GRW2 (5'-CCTGTAAAACCACCCAAC) and 1237L (5'-GAGAAACTGTGCAAAACAG). Cycling parameters were 94 C for 2 min followed by 30 cycles of 94 C for 30 sec, 56 C for 1 min, 72 C for 2 min, and a final extension at 72 C for 10 min.

As an extraction control, a primary PCR protocol that amplifies a ~813 bp region of the avian mitochondrial gene (Fain et al. 2007) was used to detect bird DNA. For amplification, 5 μl of DNA was added to 20 μl of a master mix containing 10 mM Tris-Cl (pH 8.3), 50 mM KCl, 1.5 mM $MgCl_2$, 0.2 mM each dNTP (Promega, Madison, Wisconsin), 2.5 units Taq DNA Polymerase (Promega), and 0.8 μM of primers L3827 (5'- GCAATCCAGGTCGGTTTCTATC) and H4644 (5'- TCRAATGGGGCTCGGTTKGTYTC). Cycling parameters were 94 C for 2 min followed by 35 cycles of 94 C for 30 sec, 55 C for 20 sec, 72 C for 1 min and 20 sec, and a final extension at 72 C for 7 min.

To prevent and detect contamination, the DNA extractions, primary and secondary amplification, and product analysis were done in separate dedicated areas. A negative water control was included in each set of DNA extraction, and a different water control was included in each set of primary and secondary PCR reactions. Two sex controls were included in each W-specific reaction, one from a known male (from necropsy findings) and one from a known female (egg in cloaca visible upon capture of live bird) to confirm PCR results.

Statistical analysis

I used the results of the genetic testing for each rail as the dependent variable in logistic regression models with the morphometric variables as independent predictors. I tested the six independent predictors for multicollinearity by calculating the variance inflation factor (VIF) for each and retained variables where VIF ≤ 10 (Quinn and Keogh 2002). I constructed a global model containing all parameters of interest—in this case, wing chord, exposed culmen, tail, tarsus, middle toe, and mass—plus subsets of the global model. I derived subsets of the global model using all combinations of the parameters in the Perkins et al. (2009) discriminant function, plus I included a model composed of each individual parameter I measured. I used the Hosmer-Lemeshow Goodness of Fit test to evaluate the global model (Hosmer and Lemeshow 2000) where a p-value ≤ 0.1 indicates lack of fit of the data to a logistic distribution. I compared support for the candidate models based on the data using an information theoretic approach (Burnham and Anderson 2002). I ranked models using Akaike's Information Criterion adjusted for small sample size (AIC_c) (Akaike 1973, Hurvich and Tsai 1989). The best approximating, or most plausible, model had the lowest AIC_c value and, by default, the highest Akaike weight of evidence, w_i.

Because I was interested in how well the best approximating model classified rail sexes, I calculated the classification error rate of the South Atlantic Coast birds used to build the morphometric models. Classification errors reflected when a bird of a known sex was predicted incorrectly. I established a cut-off value of 0.5 such that predictions ≥ 0.5 were classified as females and < 0.5 were classified as males. Because I was also interested in the ability of the best supported model to predict rail sex with measurements from other datasets, I estimated out-of-sample model performance using prediction error rates which measure how often the model incorrectly predicted the sex of a rail. I used morphometric data from 23 Gulf Coast clapper rails with genetically verified sexes (Perkins 2007) in the best approximating logistic model from this study to predict the sex for this subspecies of clapper rail from a different geographic location.

RESULTS

I caught 83 previously unbanded clapper rails during the two years of the study (2009: n = 44; 2010: n = 39) with one recapture of a 2009 bird in 2010. I measured all birds and collected blood and/or feathers from 82 birds. The results from the genetic analyses of these tissues showed that I captured 28 females (2009: n = 13; 2010: n = 15) and 54 males (2009: n = 29; 2010: n = 25). As expected, female clapper rails were generally smaller than male clapper rails (Table 2.1).

No predictor variable had a VIF > 2.20, so I retained all morphometric measurements for the logistic regression models. The global model fit the data ($\chi^2 = 6.34$, df = 8, p = 0.609). The model predicting clapper rail sex with measurements for wing and culmen (hereafter, wing-culmen model) was best supported by the data (Table 2.2). The equation to calculate the log-odds of a bird being a female clapper rail from these predictors was:

$$\text{Log-odds}_{(\text{female})} = 54.5447 - 0.2674*\text{wing chord} - 0.2685*\text{culmen} \qquad \text{(eqn. 2.1)}$$

I used classification error rate to evaluate the wing-culmen model's performance relative to the South Atlantic Coast rail data (Table 2.3). The model misclassification rate was 17.9% for females and 9.2% for males (Table 2.3, Figure 2.1). The overall accuracy was 81.5%. The Gulf Coast data consisted of an independent data set of 23 known clapper rails with genetically verified sex. I calculated the log-odds of being female for each bird using its specific wing chord and culmen measurements (from Appendix B, Perkins 2007) with equation 2.1. The wing-culmen model correctly predicted 100% of known females and 74.3% of known males (Table 2.4). The overall accuracy was 82.6%.

DISCUSSION

Sex was determined using genetic testing of either feather calamus or blood for 82 South Atlantic Coast clapper rails. Using logistic regression to predict sex from a combination of morphometric measurements collected from live rails was moderately successful. The wing-culmen model performed best in both predicting and classifying South Atlantic Coast male clapper rails. Error rates both in classifying and predicting South Atlantic Coast female rails were almost twice as high (Table 2.3). This result may have been in part because of the imbalance in sample size: the sample size of male rails was almost twice as large as that of female rails. Larger sample sizes may improve the error rates, especially for females, but whether this potential improvement would be sufficient to depend solely upon the model for field identification of sex is presently unclear. It is also possible that female body size is subject to opposing directional selection in terms of survival and reproductive output (i.e., larger females favored for greater reproductive output; smaller females favored in survival) (Rotella et al. 2003), resulting in greater size variability and more difficult differentiation from male birds.

The similarity between the best-predicting parameters from this study and the Gulf Coast study suggests that a reliable, morphometric-based model to classify rail sex across geographic regions is possible. The Gulf Coast function included wing chord, exposed culmen, and tarsus while this study's most plausible model contained wing chord and exposed culmen. The wing-culmen model was slightly more accurate for Gulf Coast rails than for South Atlantic Coast rails and was able to predict 100% of the known Gulf Coast females. It was not possible to predict the sexes of the South Atlantic Coast rails using the Gulf Coast discriminant function because the equation was not published (Perkins 2007, Perkins et al. 2009).

Two main issues limit the broad applicability of the wing-culmen model from this study, but could be resolved with additional work. The wing-culmen model was based on clapper rail measurements from a 2,300 ha portion of one river system (Combahee River) in coastal South Carolina. Thus, the rails represent a small proportion of South Atlantic Coast rails in both numbers and geography. Further, I assumed that all rails captured were members of the subspecies *R. l. waynei*, but some rails may have been the northern subspecies *R. l. crepitans*. I captured rails in late January/early February through June of each year, meaning some early caught rails could have been winter migrants of the other subspecies.

CONCLUSION

Predicting clapper rail sex from living birds is reasonable based on results from the wing-culmen logistic regression model and the discriminant function from the Gulf Coast study (Perkins et al. 2009). The wing chord and exposed culmen (and possibly the tarsus) are the best measurements to distinguish between males and females. The Gulf Coast discriminant function is still untested across regions. Until additional data from both regions are collected, modeled, and compared to improve the predicting equation(s), an interim solution is available. For example, for South Atlantic Coast clapper rails, the wing-culmen model could be used to calculate the log-odds and probability of being female. A subset of rails with probabilities near the cut-off value of 0.50 could be sexed genetically. Although this strategy would not eliminate the wait for lab results, costs would be reduced from fewer tests run.

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Table 2.1. Means (standard errors) for body measurements of genetically sexed female (n = 28) and male (n = 54) clapper rails captured in South Carolina during 2009 and 2010.

	Mass (g)	**Wing chord (mm)**	**Exposed culmen (mm)**	**Tail (mm)**	**Tarsus (mm)**	**Middle Toe (mm)**
Females	238.46 (7.72)	139.21 (0.98)	59.28 (0.55)	57.46 (0.82)	49.59 (0.47)	41.79 (0.66)
range	175 to 323	128 to 151	52.3 to 64.0	49 to 68	44.8 to 55.1	34.0 to 47.3
Males	275.15 (4.81)	149.43 (0.73)	64.71 (0.48)	60.94 (0.70)	53.46 (0.49)	44.94 (0.71)
range	205 to 344	135 to 160	56.7 to 72.4	52 to 79	43.8 to 60.1	36.0 to 55.6

Table 2.2. Candidate logistic regression models to predict clapper rail sex ranked using second order Akaike's Information Criterion (AIC_c) and Akaike weights (w_i), where K is the number of parameters.

Model	**K**	**AIC_c**	**Δ AIC_c**	**w_i**
wing + culmen	3	59.704	0	0.644
wing + culmen + tarsus	4	61.490	1.786	0.264
wing	2	63.888	4.184	0.080
global model	7	68.066	8.362	0.010
culmen + tarsus	3	71.454	11.750	0.002
culmen	2	74.295	14.591	0
tarsus	2	89.163	29.459	0
mass	2	95.410	35.706	0
tail	2	101.912	42.208	0
toe	2	103.370	43.666	0
null model	1	109.440	49.736	0

Table 2.3. Rows in the confusion matrix for the wing-culmen model show the proportion of times the model incorrectly sexed a South Atlantic Coast clapper rail of known sex was (i.e., the classification error rate).

	predicted male	predicted female	**classification error rate**
known male	49	5	**9.2%**
known female	5	23	**17.9%**

Table 2.4. Columns in the confusion matrix for the wing-culmen model show the proportion of times the model incorrectly predicted a Gulf Coast clapper rail sex (i.e., the prediction error rate).

	predicted male	predicted female
known male	11	0
known female	4	8
prediction error rate	**26.7%**	**0.00%**

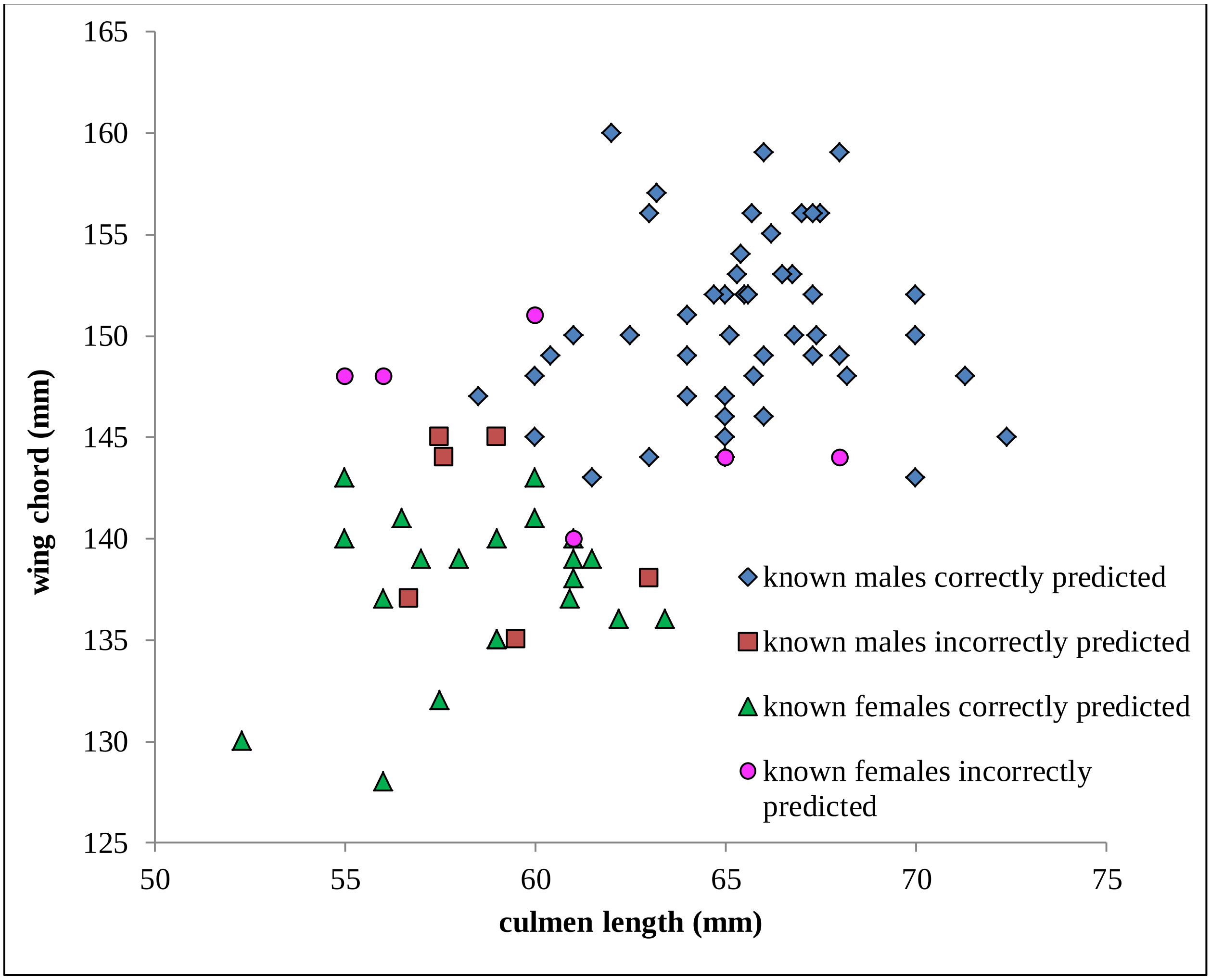

Figure 2.1. Predictions of South Atlantic Coast clapper rail sex by the wing-culmen logistic regression model and agreement with genetically determined sex.

CHAPTER 3

HABITAT SELECTION AND IMPLICATIONS FOR SURVIVAL OF SOUTH CAROLINA CLAPPER RAILS (*RALLUS LONGIROSTRIS*)[1]

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[1] Ricketts, C. E., J. Hepinstall-Cymerman, W. E. Mills, R. J. Cooper, S. H. Schweitzer, and E. P. Wiggers. To be submitted to *Journal of Wildlife Management*.

ABSTRACT

Habitat selection studies are enhanced by investigating demographic outcomes for individuals within their selected habitat. The clapper rail (*Rallus longirostris*) along the Atlantic Coast is a game species for which there is copious qualitative habitat data and some quantitative data, but no estimates of survival. Here we evaluated the home range selection of 54 rails by comparing landscape and local scale habitat metrics between observed and simulated home ranges. Males and females occupied home ranges of similar sizes and habitat characteristics. Food availability may drive home range choice; observed home ranges contained more foraging area than simulated sites. At local sampling points within sites, we found that observed home ranges contained higher percent bare ground, which may approximate home-range wide food availability, than simulated sites. Survival probability for 2009 males was 0.74 (n = 29); for females, 0.69 (n = 13). In 2010 survival probability for males was 0.94 (n = 25); for females, 0.93(n = 15). For 2009 only, survival models including habitat covariates suggested increased survival with increased foraging area and decreased survival with increasing bare ground.

Key words: clapper rail, home range selection, adult survival, adaptive local convex hull

INTRODUCTION

More than 1.2 million hectares of U.S. wetlands were converted to other land uses during the last 30 years of the 20th century (Dahl and Johnson 1991, Dahl 2000, Dahl 2006, Cooper 2007). In coastal areas, these land use alterations, combined with current threats from invasive plants, fragmentation, pollution, siltation, dredging, and channelization can negatively impact resident tidal marsh species (Cooper 2007, Cumbee et al. 2008). Projected changes to coastal marshes from sea level rise will only add to the challenges faced by these organisms (Erwin et al. 2006, van de Pol et al. 2010). Mitigation of wetland loss or degradation using constructed wetlands, including marshes, does not guarantee such habitats are capable of sustaining marsh obligate species (Boyer and Zedler 1998, Melvin and Webb 1998, Desrochers et al. 2008).

Here I define “habitat” as the space containing the physical resources and environmental conditions necessary for a particular organism to survive, at minimum (Block and Brennan 1993). High quality habitats enable individuals not only to survive, but also to reproduce and enable local populations to persist (Hall et al. 1997). To conserve or create high quality habitat is an important goal of researchers and land managers concerned with resident species of coastal marsh ecosystems. Poor human accessibility to tidal marshes has resulted in low spatial coverage in surveys of secretive avian species. Low detection rates with high variability (e.g., observed coefficient of variation of 189%) compound the inadequate sampling coverage, further reducing precision in population modeling efforts (Gibbs and Melvin 1993, Conway and Gibbs 2005). Moreover, the presence of individuals at a site does not indicate a high quality habitat unless supported by corroborating demographic evidence (Van Horne 1983, Pulliam 1988). For some marsh species these factors have resulted in a severely limited understanding about basic demographic rates, population trends, and specific habitat requirements (MSUGBSTF 2009).

One may assess habitat quality through analysis of habitat use patterns that result from habitat selection processes (e.g., Jones 2001) where individuals select some habitat over others. Biotic and abiotic factors both influence the selection of a home range (Jones 2001, Horne et al. 2008) and the likelihood of survival and reproduction within that space (e.g., Schmitz and Clark 1999). Habitat selection is hierarchical with choices at broader scales constraining those at finer scales (Johnson 1980). For example, a species' geographic range represents first-order selection and a home range placement within that range constitutes second-order (Johnson 1980).

Telemetry data have proven useful in answering questions about second-order selection in general, and specifically habitat selection, use, and quality in marsh ecosystems (Legare and Eddleman 2001, Cumbee et al. 2008). These data allow researchers to define home range boundaries, within which animals ideally find adequate resources to fulfill their seasonal life history requirements. Data collected from radio-marked animals can also be used to estimate survival and assist in the discovery of nest sites, facilitating studies of reproductive output.

An area of active research is how to describe most accurately an animal's home range selection (Thomas and Taylor 2006, Aarts et al. 2008, Laver and Kelly 2008, Long et al. 2009). One common strategy is to compare quantities and qualities of used to available habitats using logistic regression (Manly et al. 2002). Available habitat is considered to be all habitat within an area, typically human-defined (Thomas and Taylor 2006), regardless of use by the study organism (Jones 2001). That is, the habitat, by definition, could be used by the animal, but may not be in use currently. Often, it is not possible to determine "unused" areas with complete certainty (e.g., surveying versus censusing a population). The outcome of the used-available comparison is a resource selection function (RSF) which is proportional to the use probability. Despite a theoretical concern about the validity of the RSF and potential bias from sample contamination (i.e., some available habitat also “used”) (Keating and Cherry 2004), this analysis strategy remains robust (Johnson et al. 2006).

One coastal marsh species for which little quantitative survival, habitat selection, use, and home range data exist is the clapper rail (*Rallus longirostris*). Clapper rail populations are believed to be stable along the Atlantic coast, although habitat loss and degradation are ongoing concerns (Eddleman and Conway 1998). The natural history of eastern clapper rails has been well documented, especially for the Carolinas and Georgia (e.g., Oney 1954, Adams and Quay 1958, Blandin 1963, Meanley 1985, Gaines et al. 2003) but current estimates of local or regional population numbers and of basic demographic parameters are non–existent (MSUGBSTF 2009), mainly because historical data are lacking (Cooper 2007). Data collected from previous studies is insufficient to quantify retroactively the relationship between habitat and demographic outcomes to assess habitat quality.

Previous efforts measured the amount of habitat individual rails require but sample sizes were low. Breeding clapper rails exhibit territorial behavior (Lewis and Garrison 1983) and intraspecific competition likely impacts their densities and home range sizes. In Georgia, breeding density of clapper rails was 2.2 to 3.7 birds per ha; fall density was 3.2 birds per ha (Oney 1954). Mean breeding season home range size, calculated using 100% minimum convex polygon (MCP), was 1.2 ha for seven birds (Cumbee et al. 2008). In coastal South Carolina, breeding season MCP home range sizes for two birds were 7.3 ha and 0.4 ha (McGregor 2007). Another study examined seasonal changes in habitat use. In North Carolina, clapper rails shifted their summer home ranges in low-marsh dominated by smooth cordgrass (*Spartina alterniflora*) and black needlerush (*Juncus roemerianus*) to winter home ranges in high-marsh dominated by saltmeadow cordgrass (*Spartina patens*) (Adams and Quay 1958). No formal link between any of the habitat data and survival of the birds was investigated, nor were statistical comparisons made between used and available areas. The habitat quality of these study areas is therefore unknown and little of this information can be applied to assess or improve existing rail habitat.

Other studies provide a foundation upon which to formulate habitat selection and use hypotheses. The distance to a tidal river or creek is a reliable indicator of clapper rail presence (Lewis and Garrison 1983) and may relate to food availability. A habitat suitability index (HSI) identifies the most suitable habitat to be marsh lands within 15 m of water's edge (Lewis and Garrison 1983) based on these areas being suitable foraging habitat. Fiddler crabs (*Uca* spp., *Sesarma* spp.) and periwinkle snails (*Littoraria* spp.) are two of the most important prey items for rails (Oney 1951, Lewis and Garrison 1983, Meanley 1985, Rush et al. 2010b). During low tide periods, clapper rails move closer to the exposed banks of a tidal waterbody to forage (Meanley 1985, Rush et al. 2010a). Based on call-count surveys, vegetation height and species corresponded to abundance of clapper rails in New Jersey, but no explicit test of the cause of this association was conducted (Mangold 1974). Rails were most abundant in shorter smooth cordgrass marshes than in taller smooth cordgrass marshes or in marshes of mixed vegetation types (Mangold 1974). High interspersion, defined as the amount of edge at the vegetation–water interface (Rehm and Baldassarre 2007), can indicate presence of secretive marsh species such as the Virginia rail (*R. limicola*), sora (*Porzana carolina*), and least bittern (*Ixobrychus exilis*) (Rehm and Baldassarre 2007), and may also indicate clapper rail presence.

The goal of this work was to develop a more complete understanding of habitat selection (second-order or home range selection) and use by clapper rails and the resulting impact on adult survival. Specific objectives included: 1) estimate home range size from telemetry data collected from radio-marked birds; 2) determine what variables drive home range selection through a comparison of observed (used) home ranges versus what is available on the landscape (i.e., within simulated home range sites); and 3) estimate adult survival with respect to home range selection. My hypothesis for objective one was that season affected a clapper rail home range size more than the sex of the bird. Non-breeding season home ranges would be larger than breeding season home ranges; within each season home ranges sizes would be similar between male and female rails. My hypothesis for objective two was that a clapper rail's choice of a home range site would minimize travel distances to feeding areas, maximize feeding areas, and maximize cover from predators by including taller vegetation. Specifically, the mean distance to an edge, vegetation height, and the amount of foraging area within a home range are the most important predictors home range placement (i.e., of observing a home range at a specific location). Within observed home ranges (i.e., "used" home ranges), mean distance to an edge is shorter, vegetation height taller, and the amount of foraging area greater than within simulated home ranges (i.e., "available" home ranges). My hypothesis for objective three was that clapper rail home ranges are situated so that they contain the necessary resources for a bird to escape from predators and find food. Habitat covariates related to these resources are important predictors of adult survival, but the sex of the bird is not an important predictor. Greater stem density, taller vegetation height, and greater amounts of foraging area are correlated to higher survival probabilities for adult rails.

STUDY AREA

The Ashepoo-Combahee-Edisto (ACE) Basin in southern coastal South Carolina is largely rural (Coastal Services Center 2000) and provides an opportunity to conserve and restore habitat for marsh bird species (Tufford 2005). Part of the Basin is within the National Oceanic and Atmospheric Administration's (NOAA) National Estuarine Research Reserve System (NERRS) and contains land protected through the cooperation of state, federal, private, and nonprofit interests (Coastal Services Center 2000).

In this study I focused on an approximately 2,300 ha portion of tidal marsh along the Combahee River and Wimbee Creek within the ACE Basin (Figure 3.1). The northern boundary of the study area is formed by the U.S. 17 bridge crossing the Combahee River which also delineates the legal transition from salt to fresh water. The study area is approximately 8 km north to south and covers a range of salinity values (W. E. Mills, personal communication). The southern boundary is the Wimbee Creek boat landing. The western boundary abuts the marsh edge primarily along the Nemours Plantation Wildlife Foundation property line while the eastern boundary is formed by other private plantation property lines adjacent to the Combahee River. Smooth cordgrass dominates the marsh of these two connected water bodies. Black needlerush forms largely homogeneous patches mainly in the northern portion of the study area and also in higher elevations throughout. Saltmarsh bulrush (*Schoenoplectus robustus*), big cordgrass (*Spartina cynosuroides*), and soft-stemmed bulrush (*Schoenoplectus tabernaemontani*) are interspersed with smooth cordgrass, mainly in the northern portion of the study area while saltmarsh aster (*Symphyotrichum tenuifolium*) is interspersed with smooth cordgrass throughout the study area (personal observation). In coastal South Carolina, tides are semidiurnal with a higher high water and a lower low water. Diurnal tidal range is approximately 2.29 m.

METHODS

Rail capture and telemetry

I captured clapper rails throughout the study area during night-time spring tides between January and June in both 2009 and 2010. I searched areas via airboat where I had previously detected the birds during informal surveys of the study area prior to catching events. One person scanned the marsh with a thermal imaging camera (Thermal-Eye 250D or X200xp, L-3 Communications Infrared Products, Dallas, Texas) for a heat signature indicating the presence of a rail. The camera-person directed the airboat driver to the location while another person, plus myself, carried spotlights and dip-nets to capture the rails (Mills et al. 2011).

I collected morphometric measurements from each rail including body mass and lengths of exposed culmen, un-flattened wing chord, middle toe, tarsus, and tail (Appendix A). I also collected the 7th primary feather from one wing and several rectrices for genetic analysis. In addition, in 2010 I collected a blood sample from the brachial vein for genetic and parasitic analyses. I outfitted each rail with a radio-transmitter equipped with a mortality signal (Wildlife Materials model SOPB 2190 M, Murphysboro, IL; or Holohil Systems model RI-2CM, Carp, Ontario, Canada) that was ≤ 4% of the bird's body mass as suggested by Raim (1978). I custom-fit each transmitter to the rail by tying the device in a backpack-style using thin elasticized cord (Haramis and Kearns 2000).

I traversed the study area using a john boat and tracked clapper rails using an ATS receiver (Model R4000, Advanced Telemetry Systems, Inc. Isanti, Minnesota) with a handheld 3-element Yagi antenna (148–151.999 MHz). I located individuals at different hours (daylight and dark) and tidal heights throughout the season. I remained in the boat when tracking a rail to minimize disturbance to marsh lands and the individual. I recorded positions using a handheld GPS unit (Garmin Corporation, Olathe, Kansas) where error was ≤ 5 m for each fix. I either estimated distance to the bird (when I could approach the bird as close as possible) or triangulated its location (when accessibility to the bird's location was limited, e.g., by low tide) (White and Garrott 1990). I used Locate 3.33 (Pacer Computing, Nova Scotia, Canada) to convert the raw coordinates to actual bird locations. In both years I estimated the accuracy of the effort to locate clapper rails using telemetry. I placed a transmitter at locations throughout the study area and recorded its positions with a GPS. Later, I returned to "track" this transmitter using the receiver and antenna and recorded my estimate of its actual location. I calculated the distance between the actual location and my estimate to calculate the mean distance error inherent in my relocation efforts.

From time of initial capture (earliest Jan. 31) until mid-July of each year I recorded between two to six fixes per week for each bird by tracking at least five days per week. From mid-July to the 1st week of August I recorded one to two locations per bird each week. A minimum of 12 hours passed between subsequent fixes. If I detected a mortality signal, I attempted to retrieve the transmitter and the bird to determine cause of death. If I did not detect a bird near its normal locations, I searched the study area on multiple occasions to relocate it. I expanded the search beyond the study area boundaries when the normal locations of the missing individual were near the edge of the study area. Between late March and early June 2010, W.E. Mills scanned the frequencies of missing clapper rails during seven fly-overs of the study area and beyond (W. E. Mills, personal communication).

Observed (used) and simulated (available) home range construction

I used the adaptive local convex hull (a-LoCoH) method to calculate a home range for each bird (Figure 3.2) for individuals with >13 recorded locations (Cumbee et al. 2008). A-LoCoH creates convex "hulls" from data points where the smallest hulls represent the most intensely used portions of a home range. By combining these hulls from smallest to largest the resulting boundary equals the isopleth of interest, e.g., 90% isopleth contains 90% of the data points (Getz et al. 2007). Instead of a employing a fixed distance or fixed number of points from a root point to construct each hull, the adaptive method uses a variable distance from the root point, thereby more clearly delineating areas of high use (Getz et al. 2007).

A-LoCoH has several advantages over kernel methods for home range construction. First, a-LoCoH is a nonparametric technique and thus requires no user-assigned functional form to data that may be multimodal or clustered (Getz et al. 2004). Additionally, a-LoCoH area estimates converge with increasing numbers of points, which is generally untrue in kernel methods (Getz et al. 2007). When delineating clapper rails' use of the tidal marsh system, a-LoCoH has demonstrated capacity to account for hard edges (e.g., rivers) in home ranges where kernel methods generally fail to delineate edges (Getz et al. 2007). To estimate each home range area I used the 90% isopleth to reduce bias from smaller sample sizes (Borger et al. 2006, Getz et al. 2007).

I also calculated the 100% MCP home range for each bird for two reasons. First, earlier studies used this technique thus facilitating comparisons between this work and earlier projects. Second, I compared the local habitat variables measured solely within the 90% isopleth to those measured outside the 90% isopleth boundary but within the 100% MCP boundary. Observed differences between these sets of metrics imply differential use of the home range.

Using GIS (ArcGIS 9.3, ESRI, Redlands, California) I established a set of 85 random points throughout the study area to serve as centroids (center points), around which I simulated a clapper rail home range (Figure 3.3). Because my sample of radio-marked clapper rails did not represent a census of the population in the study area, I can only make comparisons between observed (i.e., used) home ranges and simulated (i.e., available) home ranges rather than the more statistically valid comparison of used versus unused home ranges. I ensured the distribution of area values for the simulated home ranges approximated the distribution of area values for the observed home ranges: area values for 25% of simulated home ranges were within each quartile of observed home range area values. I distributed these area values for the simulated home ranges approximately equally between two different home range shapes, hexagon and diamond, which approximated the observed home range shapes from the telemetry data points. Simulated home ranges did not overlap observed home ranges.

Landscape variables

I created habitat variables for each observed and simulated home range (Table 3.1). I used aerial photographs of the study area from 2006 (taken near low tide) and 2009 (taken near high tide) to determine the amount of foraging area present, the amount of land area present, and the mean distance to an edge (i.e., foraging location) across each home range. To estimate foraging area, I digitized rivers and streams within and adjacent to the observed and simulated home range sites using ArcGIS. By digitally tracing the outline of the exposed riverbanks and creeks drained during low tide, I could quantify the amount of exposed mud flats available in each site (Figure 3.3). By subtracting the amount of foraging area from the total area I also determined the amount of marsh land in each site. I natural log transformed each of the two area variables for statistical analyses (see below). I also used the digitized waterways to find the mean distance to an edge (i.e., a foraging site) in each home range. Again using ArcGIS, I calculated the Euclidean distance for all points (1 m cells) within a home range to an edge, represented by the digitized waterway polygons. From this raster I calculated the mean distance to an edge (foraging site) for each home range.

Local variables

I measured habitat variables in the field within a 0.50 m^2 sampling frame (the local scale). These variables included distance to nearest edge (foraging site), mean vegetation height, number of stems (i.e., stem density), species present, percent bare ground, and percent cover of each species observed (Table 3.1). Within each observed home range I collected data at 10 random points. I measured the same habitat variables at 36 random locations outside the observed home ranges. These 36 points were used as centroids for 36 of the 85 simulated home ranges.

Statistical analyses

I created cumulative frequency distributions to visually examine the relationship between observed and simulated home range sites for each habitat variable. I also checked for multicollinearity of the variables to verify independence, retaining those where correlations resulted in $r^2 < 0.6$ (Fielding and Haworth 1995).

Observed (versus simulated) home ranges served as my dependent variable in logistic regression models with habitat variables as independent predictors of home range selection. I constructed models representing different biological hypotheses about habitat selection by clapper rails that included local and landscape variables for the amount and configuration of foraging habitat as well as local vegetation structure (Table 3.2). For comparison, I included a global model containing all parameters of interest, plus the null (intercept-only) model in the candidate set of models. I used the Hosmer-Lemeshow Goodness of Fit test to evaluate the global model; a p-value ≤ 0.1 indicates lack of fit of the logistic form to my data (Hosmer and Lemeshow 2000).

I compared support for the candidate models based on the data using an information theoretic approach (Burnham and Anderson 2002). I ranked models using Akaike's Information Criterion adjusted for small sample size (AIC_c) (Akaike 1973, Hurvich and Tsai 1989). The confidence set of models (i.e., those models best supported by the data) included all models where $\Delta\ AIC_c \leq$

2 (Burnham and Anderson 2002). If no models were within Δ $AIC_c \leq 2$ of the top-ranked model then I used only the top-ranked (i.e., best approximating, lowest AIC_c value) for inference.

If the confidence set of models contained > 1 model, I calculated model-averaged estimates for those parameters present in the confidence set to create a composite model of habitat selection. I weighted each parameter estimate by the Akaike weight, w_i, from every candidate model in which it appeared and then summed these weighted values for the model-averaged estimate (Burnham and Anderson 2002). I also calculated 95% confidence intervals for these model-averaged parameter estimates. In this case, I based all inferences on the composite model. I calculated importance weights—the summed Akaike weights across all candidate models containing a specific parameter—for each covariate in the composite model. Importance weights provided insight into the most influential parameter(s) on the response variable given the data and the candidate models.

To aid in interpretation and comparison of each predictor variable's effect on habitat selection, I computed scaled odds-ratios for parameter estimates and confidence intervals of the best approximating or composite model (Hosmer and Lemeshow 2000). I calculated scaled odds-ratios for two reasons. First, scaling the odds-ratios facilitates a comparison of effect on the response variable among parameters with different units. Second, a scaled odds-ratio for a parameter estimate can reflect a more biologically meaningful change in the response variable. An unscaled odds-ratio describes the impact of a one-unit change on the response variable. In this system, for example, it is more realistic biologically to consider the scaled effect of a 10 m decrease (versus a 1 m decrease) in mean distance to edge on the increased probability of an observed home range site.

I modeled weekly adult survival using Pollock's staggered entry design (Pollock et al. 1989) in Program MARK version 6.1 (White and Burnham 1999). I considered each year separately. With this design I was able to estimate different survival probabilities for trapping occasions spaced irregularly throughout both years. I considered all clapper rails radio-marked on the same trapping occasion as part of a unique "release-group." Because I determined the sex of each rail with genetic testing (see Chapter 2), I included sex as a covariate. First, I developed candidate models including release-group and sex effects, without habitat covariates, for each year to capitalize on the larger sample size of radio-marked rails available for this analysis (Table 3.3). I ran a second set of survival analyses on the subset of rails for which I was able to construct home ranges and had used in the habitat selection modeling above. Here I included not only release-group and sex effects but also the most important habitat variables identified in the best approximating habitat selection model (Table 3.4). I ranked my adult survival models using AIC_c (Akaike 1973, Hurvich and Tsai 1989) using the same methods described above.

RESULTS

General home range results

I caught and radio-marked 83 previously unbanded clapper rails during the two years of the study (2009: n = 44; 2010: n = 39) with one recapture of a 2009 bird in 2010. Results from the genetic analyses of collected tissues (see Chapter 2) showed that I captured 28 females (2009: n = 13; 2010: n = 15) and 54 males (2009: n = 29; 2010: n = 25). Mean distance error in the telemetry accuracy assessment was 41.99 ± 10.08 m (range: 0.89 m to 373.75 m; n = 56).

I was unable to capture the pre- and post-breeding season locations of rails with sufficient detail for statistical analysis. I obtained a larger sample of pre-breeding (February to mid-March) telemetry data in 2009 compared to 2010. During this period in 2009, several male birds made evident shifts from one marsh area to another where they remained for the rest of the study period (i.e., the breeding season). Areas inhabited before and after the shift were of similar sizes and dominated by smooth cordgrass. These movements were different than those documented in North Carolina where birds shifted from high marsh to low marsh (Adams and Quay 1958), but those movements were also seasonal: winter versus summer.

Rails generally remained in the same home range area throughout the breeding period (mid-March to mid-August). I created breeding season home ranges for 57 rails using a total of 2,407 individual locations (mean number of points per home range = 42; range: 14 to 78). Of these 57 home ranges, I used 54 in the selection analysis: I excluded one home range that consisted of locations obtained only during the pre-breeding season; I excluded two additional home ranges each of which had disjunct polygons for the 90% isopleth. The disjunct polygons did not, however, represent a shift by either bird from one location to another and including them would result in two home range samples per bird.

Of the 54 useable home ranges, there were 8 female home ranges and 14 male home ranges in 2009 and 12 female and 20 male home ranges in 2010. For the 22 home ranges in 2009 and the 32 home ranges in 2010, there were no significant differences between male and female rails for any of the habitat variables (t-tests: df = 52, all $p > 0.156$) or in size of home range ($t = 0.158$, df = 52, $p = 0.875$). However, in 2009, area of home ranges, amount of land area, and mean distance to edge for all birds combined was significantly larger than in 2010 (Table 3.5). In 2009, both mean vegetation height and percent bare ground were significantly lower than in 2010 (Table 3.5).

The cumulative frequency distribution (CFD) comparing the size (natural log transformed) of observed and simulated home ranges showed that I generally matched the distribution of simulated home ranges to the observed home ranges (Figure 3.4A). The observed and simulated home range areas were not significantly different (t = 0.287, df = 137, p = 0.774). At the landscape scale, observed home ranges generally had more foraging area than simulated home ranges (Figure 3.4B), but similar land area (Figure 3.4C), suggesting that the amount of foraging area was more important than land area when rails selected home range locations. Observed home range sites exhibited significantly shorter mean distance to edge (i.e., foraging site) than simulated sites (Table 3.1, Figure 3.4D). On average, an edge (foraging site) was only 9.89 m away from any point in an observed site.

At a local scale, the distance to edge (i.e., a foraging site) was shorter in observed home ranges versus simulated home ranges (Figure 3.5A). Percent bare ground was greater in the observed sites versus simulated sites (Figure 3.5B) and, stem density was slightly lower in observed sites compared to simulated (Figure 3.5C). Vegetation height range was narrower in observed sites than simulated (Figure 3.5D).

I found differences in habitat characteristics when comparing measurements between those points sampled within the 90% isopleth and those points sampled outside the 90% isopleth but within the 100% MCP boundary. The distance to edge was significantly shorter (p = 0.002, t =3.111, df = 106) between points measured solely within the 90% isopleth compared to those measured outside the 90% isopleth but within the 100% MCP (Figure 3.5A). Stem density (Figure 3.5C) was slightly lower within the 90% isopleth than outside the 90% isopleth but within the 100% MCP. Mean vegetation height (Figure 3.5D) tended to be taller within the 90% isopleth. Percent bare ground was essentially equal throughout an observed home range (Figure 3.5B).

Logistic regression results

None of the predictor variables were correlated, so I retained all habitat variables for the logistic regression models. The global model fit the logistic distribution (Hosmer-Lemeshow GOF $\chi^2 = 3.343$, df = 8, p = 0.911).

The most plausible model explaining clapper rail home range selection within the study area was the foraging model with 87% of the Akaike weight (Table 3.6). This model was 7.0 times more likely than the next best approximating model, the distance-and-foraging model with 12% of the weight. Because no other model had an AIC_c value within 2 of the AIC_c value of the foraging model, I used only the foraging model for inference (Burnham and Anderson 2002).

The more foraging area present in a site, the more likely the site was an observed clapper rail home range. As foraging area increased on a natural-log scale, an observed home range (versus simulated) was 1.9 times more likely (Table 3.7). Similarly, the percent of bare ground at sampling locations had a positive relationship with observed home ranges. For each 10% increase in the amount of bare ground, a sampling location was 1.8 times more likely to be within an observed home range versus within a simulated home range.

Foraging area was greater in observed home ranges than in simulated sites (Table 3.1, Figure 3.4B) and this metric did occur in the most plausible habitat selection model (Table 3.7), supporting my prediction. Mean distance to an edge (i.e., mean distance to a foraging site) in observed home ranges was shorter than in simulated home range sites (Table 3.1, Figure 3.4D) but this variable was not present in the best supported logistic regression model; instead, it was present in the second-ranked model with 12% weight. Mean vegetation height was not different between observed and simulated sites (Table 3.1, Figure 3.5D) nor was it present in the best supported model.

Adult survival results

In 2009, I confirmed 11 rail mortalities, six females and five males. I tracked three radio-transmitters to a nearby bald eagle (*Haliaeetus leucocephalus*) nest. It is unknown whether the eagle scavenged or directly killed the rails. I tracked another transmitter to a spot near a great horned owl (*Bubo virginianus*) nest. The causes of the remaining deaths were unknown. In 2010, I confirmed three rail deaths, two males and one female. I recovered two carcasses and transmitters in the marsh near where I had released the birds (see Appendix B for one necropsy report) and the third bird I tracked to an eagle's nest. In each year, a majority of the birds' signals disappeared (n = 25 in 2009; n = 24 in 2010; were censored) from the study area. Despite extensive searching by boat, automobile, and plane (in 2010 only) these missing individuals were not rediscovered. Some of the censored birds, especially those lost earlier in 2009, may have been migrants of the subspecies *R. l. crepitans* returning to the Mid-Atlantic Coast from their wintering grounds in South Carolina.

The first set of analyses estimated survival from the telemetry data without habitat covariates. In 2009, I used 24 weeks of telemetry data for survival estimation of 44 clapper rails. In 2010, I used 27 weeks of data to estimate survival of 36 rails. For both years the confidence set of models contained the null model and the sex model (Tables 3.8 and 3.9). A rail's sex may impact survival but in both years standard error relative to the parameter estimate was large and the resulting confidence interval wide, leading to inconclusive results (Tables 3.10 and 3.11). Based on the composite model, in 2009, the estimate of weekly survival for male rails was 0.988 and for females, 0.985. The estimate of surviving the entire 24-week study period was 0.743 for males and 0.690 for females. In 2010, the estimate of weekly survival for male rails was 0.998

and for females, 0.997. The estimate of surviving the entire 27-week study period was 0.944 for males and 0.934 for females.

I used a subset of the radio-marked rails to estimate survival including the habitat covariates, percent bare ground and natural log-transformed foraging area which were the two parameters in the most plausible model of habitat selection. The subset consisted of 23 birds from 2009 and 29 birds from 2010. For 2009, the composite model contained the sex and both habitat covariates, percent bare ground and foraging area (Table 3.12). However, confidence intervals for each parameter included 0, preventing a conclusive statement on each one's magnitude and direction of effect on clapper rail survival (Table 3.13). In 2010, the best supported model was the null model and the sex-only model was ranked second with 20% of the weight and a ΔAIC_c of 2 (Table 3.14).

My prediction that habitat covariates would be important factors in estimating survival was not supported by the data for 2010 and was weakly supported for 2009. Contrary to my prediction, sex may be an important determinant in adult rail survival, with males having slightly higher probability of survival

DISCUSSION

Habitat selection

Clapper rail home range sizes within my study area were similar to sizes found in other Atlantic coast studies (McGregor 2007, Cumbee et al. 2008) and to a recent Gulf coast study of the subspecies, *R. l. saturatus* (Rush et al. 2010a). Home range size may change temporally (Rolando and Carisio 1999) for one or both sexes but in this study my data was insufficient to estimate seasonal differences in home range characteristics. An adjustment in home range size could coincide with a shift in habitat type as rails can exhibit seasonal plasticity in home range location, shifting between low and high marsh (Adams and Quay 1958). I documented several definitive movements by male clapper rails in early spring but these home range shifts did not represent a change in habitat type nor a large increase or decrease in area (data not shown). Overall, male and female clapper rails had equivalently sized home ranges. Because my telemetry data focused primarily on the breeding season, and it is known that both sexes incubate a nest and care for young broods (Meanley 1985), this result was expected.

Food availability is known as a major driver in the process of avian habitat selection (Rolando 2002) and is likely a major influence in this system. Clapper rails clearly selected home range sites with a greater amount of foraging area (i.e., river banks and interior tidal creeks) than present within simulated sites (Table 3.1) and this variable was a key predictor of an observed versus a simulated home range (Table 3.7). Elsewhere, distances traveled by rails from nest sites, typically located close to an edge (see Chapter 4), were reduced with increasing fiddler crab abundance, implying a smaller breeding home range size as food availability increased (Rush et al. 2010a).

Rails may concentrate near edges at low tide because they represent major foraging locations (Rush et al. 2010a), but in this study area the landscape-scale metric, mean distance to edge (foraging site) was not an important factor in distinguishing between an observed versus simulated home range, contrary to my prediction. Nor was the local-scale measurement, distance to edge, present in the best-supported model of selection. A shorter distance to edge (i.e., foraging site) in the 90% isopleth indicated a within-home range difference in use of habitat. This result suggests that the main portion of a rail's home range was focused on access to foraging areas and that the less frequently visited outer portion served another purpose (e.g., territory defense). Observed home ranges showed significantly shorter distances for both distance measurements indicating that higher quality foraging opportunities may be nearest or at an edge. Rails may select for this variable, but the impact of the amount of bare ground present, which was an important predictor of an observed home range, may drive a rail's selection more strongly than distance metrics.

The local-scale variable, percent bare ground, was higher at observed sites, but vegetation height and density were similar between observed and simulated home ranges, suggesting fine-scale patchiness within clapper rail home ranges compared to simulated sites. This patchiness may serve as a proxy indicating additional foraging opportunities. Periwinkle snail densities increase as cordgrass density increases in large marsh areas (i.e., > 0.8 ha), such as this study area, regardless of distance to a waterbody edge (Silliman and Bertness 2002, Long and Burke 2007). Cordgrass density tends to increase as distance to edge decreases (Long and Burke 2007). However, as edge distance increases, grass height decreases, leaving more ground exposed. Periwinkle snails inhabiting cordgrass shoots farther from an edge are less susceptible to marine predators like blue crabs (*Callinectes sapidus*) (Silliman and Bertness 2002) which infiltrate mainly the first 5 to 6 m of marshlands as tide waters rise (Minello and Rozas 2002). Thus, periwinkle snails are generally available to rails throughout their home ranges, and are likely more available farther from an edge where cordgrass is more dense but shorter, and the amount of bare ground is greater.

Fiddler crab densities are highest in large marsh areas where cordgrass densities are < 80 stems/0.5 m^2 regardless of distance to a waterbody edge (Long and Burke 2007). This threshold closely approximates the maximum density (85 stems/0.5 m^2) in observed home ranges in this study (Table 3.1). Higher shoot densities may impede crab movement (Long and Burke 2007) and the maximum density recorded in a simulated site was 185 stems/0.5 m^2, more than twice the maximum in an observed site (Table 3.1). Although fiddler crabs are preyed upon by blue crabs near marsh edges at high tide like periwinkle snails (Long and Burke 2007), at low tide fiddler crabs often swarm exposed mud banks (personal observation) providing a tremendous foraging opportunity for rails. Therefore, each bird's entire home range is generally hospitable to fiddler crabs and periwinkle snails but these prey items are distributed, to a certain extent, based on opposing environmental characteristics.

At the landscape-scale, a limitation in calculating the mean distance to edge (foraging site) was the aerial photographs I used to digitize the river banks and interior creeks. These photographs did not capture all the small creeks within a home range. Reflective of that, the local -scale distance to edge (foraging site) metric was shorter than the mean distance to edge (Table 3.1). Thus, the distance to edge metric which I measured on-the-ground provided increased accuracy, albeit minimal spatial coverage, of the home range area compared to mean distance to edge. Aerial photographs of the study area with improved resolution would increase the accuracy of landscape-scale metrics such as mean distance to edge.

Adult survival

A bird's sex can influence its survival as an adult (Gaston et al. 1994, Burger, Jr. et al. 1995). This study showed that clapper rail survival may depend on a bird's sex. Results of survival modeling without habitat covariates suggested an effect of sex for both 2009 and 2010; however, the effect was inconclusive in direction and magnitude. Males had a slightly higher survival probability during the study period than females. The physical cost of reproduction for females may lower their survival (Visser and Lessells 2001) even though both sexes incubate and care for broods.

The composite model of survival for 2009 that included habitat covariates suggested effects of percent bare ground and foraging area, as well as sex. Here, the confidence interval for sex was extremely large precluding an interpretation of this parameter's effect on survival. There was a possible negative relationship between the amount of bare ground and survival probability, but confidence intervals included zero so the true nature of this relationship was inconclusive. Cover is an important feature for resident marsh species which are most vulnerable to predation when foraging on exposed mud flats (Greenberg et al. 2006), but clapper rails selected home ranges with greater amounts of bare ground. Rails optimizing foraging opportunities throughout their home ranges (e.g., for periwinkle snails) may be increasing their risk of mortality. Conversely, there was a potential positive relationship between survival probability and the amount of foraging area present. Confidence intervals for this parameter estimate also included zero. However, if the relationship holds, increased survival with increased foraging area would correspond to rails' selection of home ranges with respect to this variable. Results of the 2010 analysis of clapper rail survival with habitat covariates showed inconclusive results with the null model best-supported. During 2010, one verified mortality occurred during the 27 weeks I radio-tracked the birds thus limiting a comparison between factors contributing to birds surviving versus birds dying. For both years, sample sizes for the survival modeling with habitat covariates was smaller than the actual number of birds tracked. The relationship between survival probability and specific habitat characteristics may be clarified with a sample size increase.

CONCLUSION

The selection and use of habitat determines, in part, the ability of an animal to survive and reproduce (Hall et al. 1997). Resources available within a home range ideally provide food, shelter from predators, and nesting sites. Understanding an animal's habitat selection depends not only on the assessment of habitat metrics and social interactions but also on the demographic outcome of that animal's choice (Jones 2001). In this study I examined the influence of environmental factors on clapper rail habitat selection during the breeding season and determined whether these factors impacted rail survival. No previous study of eastern clapper rails has investigated these relationships. Food availability is likely a major driver of habitat selection in this system. Clapper rails selected home ranges with greater amounts of foraging area which may have translated to a higher probability of adult survival. Rails also selected home ranges containing a higher percentage of bare ground outside the main foraging areas which may have reduced their survival probabilities. The coastal marsh environment is a landscape of trade-offs and resident species, including clapper rails, must find a balance between conflicting strategies to survive (Greenberg et al. 2006).

Research on several pertinent topics not addressed in this study would improve understanding of what constitutes high quality clapper rail habitat and thus the ability to achieve any relevant management goals. First, this study did not include an assessment of actual food availability within observed and simulated home ranges. A directed effort to quantify prey items would determine if rails' selection of home range sites is driven by food, or if the metrics identified here as important to selection indicate another factor. Second, this effort focused primarily on the breeding season. Habitat selection and survival may change within the annual cycle for these non-migratory rails. Extending the radio-tracking period to include the remainder of the year would reveal fluctuations between breeding and non-breeding season conditions. Finally, this work was conducted in one portion of coastal South Carolina's marshes. Replicating these efforts in more locations and across the full range of clapper rail marsh habitats, i.e., purely saline to brackish, will determine if rails choose habitat based on similar characteristics and how survival is impacted by those choices. In the past, studying secretive marsh species like clapper rails was difficult because the birds are not easy to capture for radio-marking. But with new trapping methodology (Mills et al. 2011) obtaining larger numbers of rails is much easier, facilitating a longer-term study over a broader geographic area.

Given the current predictions of change to coastal landscapes from sea level rise and other ongoing threats to marsh landscapes (e.g., pollution, dredging, siltation) it is important to document habitat requirements for resident species to obtain baseline information. Similarly, estimating current population sizes, distributions, demographic rates, and trends with an acceptable degree of accuracy can indicate species' responses to changes in their habitat. This work can provide some assistance to managers in developing conservation plans focused on maintaining stable rail populations. Once verified, the habitat selection model can be used to predict quality clapper rail habitat at the home range scale.

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Table 3.1. Descriptive statistics for habitat variables in observed clapper rail (CLRA) home ranges (n =54) and simulated home range sites (landscape n=85; local n=36). CLRA home range total area is the area of the 90% isopleth calculated using an adaptive local convex hull method. SE is standard error of the mean.

	CLRA mean (SE)	**CLRA range**	**Simulated mean (SE)**	**Simulated range**
Landscape variables				
Total area (ha)	1.06 (0.18)	0.04 to 8.80	1.22 (0.17)	0.05 to 8.54
Foraging area (ha)	0.27 (0.05)	0.01 to 2.04	0.18 (0.03)	0.00 to 2.35
Land area (ha)	0.79 (0.14)	0.03 to 6.77	1.05 (0.15)	0.03 to 6.43
Mean distance to edge (m)	9.89 (0.83)	3.13 to 39.56	16.48 (1.28)	2.95 to 71.56
Local variables				
Distance to edge (m)	7.29 (0.69)	0.55 to 26.15	19.05 (3.70)	0.00 to 78.20
Mean vegetation height (cm)	120.72 (2.98)	72.94 to 181.38	122.25 (4.43)	70.50 to 190.75
S. alterniflora stem density (# stems/0.50 m^2)	45.82 (1.86)	12 to 85	50.24 (5.64)	0 to 185
Bare ground (%)	59.05 (2.10)	21 to 86.20	39.24 (3.43)	5 to 76

Table 3.2. The candidate set of models of biological hypotheses used in logistic regression to assess habitat selection by clapper rails.

Hypothesis	**Model**
Global	nl foraging area + nl land area + mean edge distance + distance to edge + mean vegetation height + stem density + % bare
Null	intercept only
Landscape distance	mean edge distance
Landscape forage	nl foraging area
Landscape land	nl land area
Local Distance	distance to edge
Vegetation structure	stem density + mean vegetation height
Foraging	nl foraging area + percent bare
Local forage	percent bare
Distance and Foraging	mean edge distance + nl foraging area + percent bare + distance to edge

Table 3.3. Candidate set of Pollock's staggered entry design known-fate models for adult clapper rail survivorship used for both 2009 and 2010 radio-telemetry data. In 2009, n = 44 clapper rails; in 2010, n = 36 clapper rails. These analyses included a larger sample size of rails but no habitat covariates.

Hypothesis	**Model**
Null	intercept
Release group	intercept + group
Sex	intercept + sex
Sex and release group interaction	intercept + sex*group + sex + group
Sex and release group no interaction	intercept + sex + group

Table 3.4. Candidate set of Pollock's staggered entry design known-fate models for adult clapper rail survivorship used for both 2009 and 2010 radio-telemetry data. In 2009, n = 23 clapper rails; in 2010, n = 29 clapper rails. These analyses included habitat covariates.

Hypothesis	**Model**
Null	intercept
Release group	intercept + group
Sex	intercept + sex
Sex and all habitat	intercept + sex + percent bare ground + nl foraging area
Sex and local habitat	intercept + sex + percent bare ground
Sex and landscape habitat	intercept + sex + nl foraging area
All habitat	intercept + percent bare ground + nl foraging area

Table 3.5. Several habitat variables differed between years for observed clapper rail home ranges. Total area is the area of the 90% isopleth calculated using an adaptive local convex hull method. Values shown are means and standard errors.

	2009 (n = 22)	**2010 (n = 32)**
Landscape variables		
Total area (ha)	1.51 ± 0.34	0.68 ± 0.15
Foraging area (ha)	0.31 ± 0.08	0.24 ± 0.07
Land area (ha)	1.20 ± 0.26	0.44 ± 0.09
Mean distance to edge (m)	12.48 ± 1.55	7.65 ± 0.51
Local variables		
Distance to edge (m)	8.77 ± 1.32	5.99 ± 0.61
Mean vegetation height (cm)	113.02 ± 5.48	127.45 ± 2.68
S. alterniflora stem density (# stems/0.50 m^2)	44.47 ± 3.44	47.41 ± 1.98
Bare ground (%)	48.78 ± 2.97	67.12 ± 2.04

Table 3.6. Comparison of habitat selection candidate models using second order Akaike's Information Criterion (AIC_c) and Akaike weights (w_i), where -2* log L is the log Likelihood, and K is the number of parameters.

Model	**-2*log L**	**K**	**AIC_c**	**Δ AIC_c**	**w_i**
Foraging	84.837	3	91.119	0.000	0.869
Distance and Foraging	84.277	5	95.009	3.889	0.124
Global	83.235	8	101.058	9.938	0.006
Landscape forage	102.583	2	106.723	15.603	0.000
Local forage	98.407	4	106.883	15.764	0.000
Local Distance	104.952	2	109.093	17.974	0.000
Landscape distance	106.272	2	110.412	19.292	0.000
Null	120.84	1	122.886	31.767	0.000
Landscape land	120.603	2	124.743	33.623	0.000
Vegetation structure	119.92	3	126.202	35.083	0.000

Table 3.7. Parameter estimates (standard error), odds-ratios, lower and upper 95% confidence limits (LCL, UCL), and importance weights for the best supported model of clapper rail habitat selection. Estimated odds-ratios with an asterisk (*) denote a confidence interval not including 1.

Parameter	Estimate (SE)	Odds-ratio unit change	Estimated odds-ratio	Odds-ratio 95% LCL	Odds-ratio 95% UCL
Intercept	-6.807 (1.871)				
nl_forage	0.636 (0.219)	--	*1.889	1.230	2.900
pct_bare	0.059 (0.016)	10	*1.804	1.317	2.445

Table 3.8. Comparison of 2009 clapper rail survival candidate models using second order Akaike's Information Criterion (AIC_c) and Akaike weights (w_i), where -2* log L is the log Likelihood, and K is the number of parameters.

Model	-2*log L	K	AIC_c	Δ AIC_c	w_i
Null	93.116	1	95.127	0.000	0.560
Sex	92.069	2	96.100	0.974	0.344
Release group	89.835	5	99.990	4.864	0.049
Sex and release group	87.918	6	100.136	5.010	0.046
Sex and release group interaction	87.918	10	108.495	13.369	0.001

Table 3.9. Comparison of 2010 clapper rail survival candidate models using second order Akaike's Information Criterion (AIC_c) and Akaike weights (w_i), where -2* log L is the log Likelihood, and K is the number of parameters.

Model	-2*log L	K	AIC_c	Δ AIC_c	w_i
Null	24.6362	1	26.648	0.000	0.705
Sex	24.4453	2	28.480	1.832	0.282
Release group	23.0143	6	35.260	8.612	0.010
Sex and release group	22.7112	7	37.040	10.392	0.004
Sex and release group interaction	22.7112	12	47.640	20.992	0.000

Table 3.10. Model-averaged parameter estimates, odds-ratios, lower and upper 95% confidence limits (LCL, UCL), and importance weights for the 2009 composite adult clapper rail survival model.

Parameter	Estimate	Standard Error	Estimated odds-ratio	Odds-ratio 95% LCL	Odds-ratio 95% UCL	Importance weight
intercept	3.162	0.484				0.904
sex	0.228	0.267	1.256	0.745	2.118	0.344

Table 3.11. Model-averaged parameter estimates, odds-ratios, lower and upper 95% confidence limits (LCL, UCL), and importance weights for the 2010 composite adult clapper rail survival model.

Parameter	Estimate	Standard Error	Estimated odds-ratio	Odds-ratio 95% LCL	Odds-ratio 95% UCL	Importance weight
intercept	4.985	0.802				0.987
sex	0.176	0.419	1.193	0.524	2.714	0.282

Table 3.12. Comparison of 2009 clapper rail survival candidate models including habitat covariates using second order Akaike's Information Criterion (AIC_c) and Akaike weights (w_i), where -2* log L is the log Likelihood, and K is the number of parameters.

Model	-2*log L	K	AIC_c	Δ AIC_c	w_i
Sex	26.636	2	30.679	0.000	0.472
Sex and local habitat	26.317	3	32.402	1.724	0.199
Sex and landscape habitat	26.496	3	32.582	1.903	0.182
Sex and all habitat	25.933	4	34.077	3.398	0.086
Null	33.249	1	35.263	4.585	0.048
All habitat	32.649	3	38.734	8.056	0.008
Release group	29.952	5	40.168	9.490	0.004

Table 3.13. Model-averaged parameter estimates, unconditional standard errors, lower and upper 95% confidence limits (LCL, UCL), and importance weights for the 2009 composite adult clapper rail survival model with habitat covariates.

Parameter	Estimate	Standard Error	95% LCL	95% UCL	Importance weight
intercept	2.960	2.748	-2.425	8.345	0.854
% bare ground	-0.009	0.019	-0.046	0.027	0.199
nl foraging area	0.057	0.163	-0.262	0.377	0.182
sex	18.039	2743.437	-5359.097	5395.175	0.854

Table 3.14. Comparison of 2010 clapper rail survival candidate models including habitat covariates using second order Akaike's Information Criterion (AIC_c) and Akaike weights (w_i), where -2* log L is the log Likelihood, and K is the number of parameters.

Model	-2*log L	K	AIC_c	Δ AIC_c	w_i
Null	0	1	2.013	0.000	0.549
Sex	0	2	4.038	2.025	0.200
All habitat	0	3	6.076	4.063	0.072
Sex and local habitat	0	3	6.076	4.063	0.072
Sex and landscape habitat	0	3	6.076	4.063	0.072
Sex and all habitat	0	4	8.127	6.114	0.026
Release group	0	5	10.191	8.178	0.009

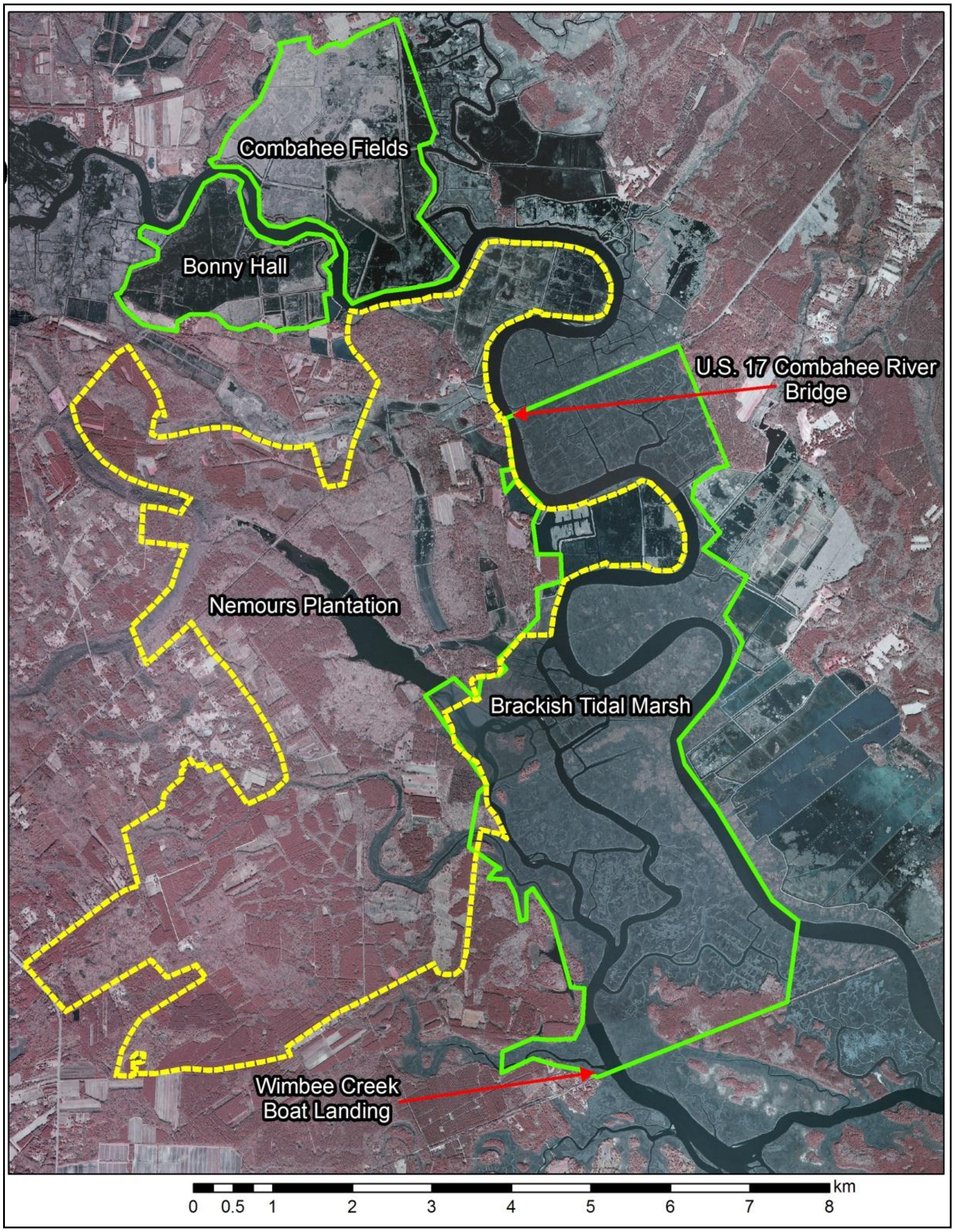

Figure 3.1. Map of clapper rail study area showing brackish tidal marsh abutting Nemours Plantation. The U.S. 17 Combahee River Bridge formed the northern boundary of the study area. The Wimbee Creek Boat Landing is the southernmost extent of the study area.

Figure 3.2. Map depicting 90% isopleth boundary of the observed home range for clapper rail #33176 (aka Cruella). The home range boundary and Cruella's locations overlay the 2006 imagery which shows the exposed riverbanks and drained creeks seen across the marsh during low tide periods.

Figure 3.3. Map depicting a simulated home range boundary constructed around a centroid randomly placed within the study area. Foraging areas are outlined for use in calculating mean distance to edge, amount of land area, and amount of foraging area within each home range.

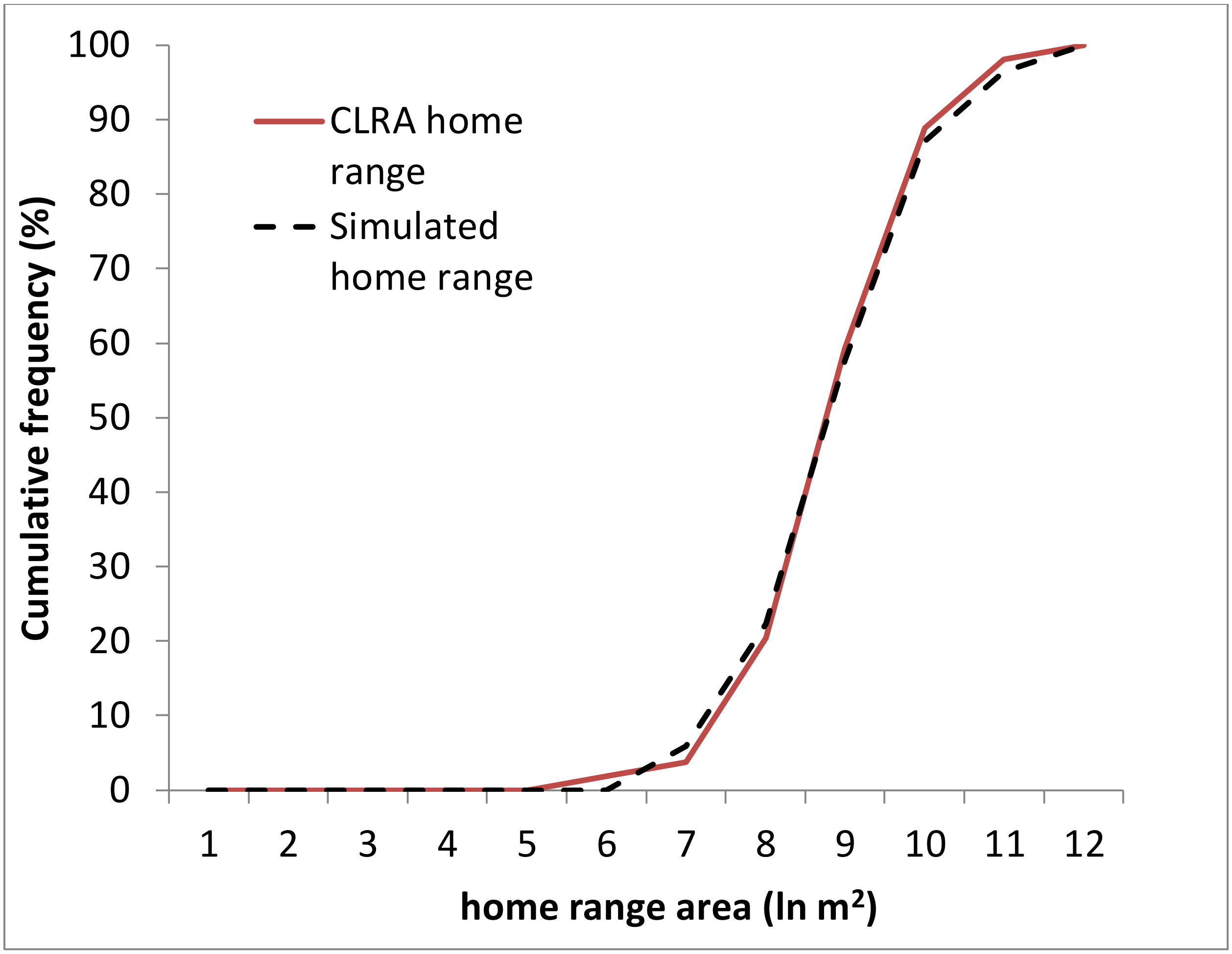

Figure 3.4A. Distributions of natural log transformed areas of observed and simulated home ranges.

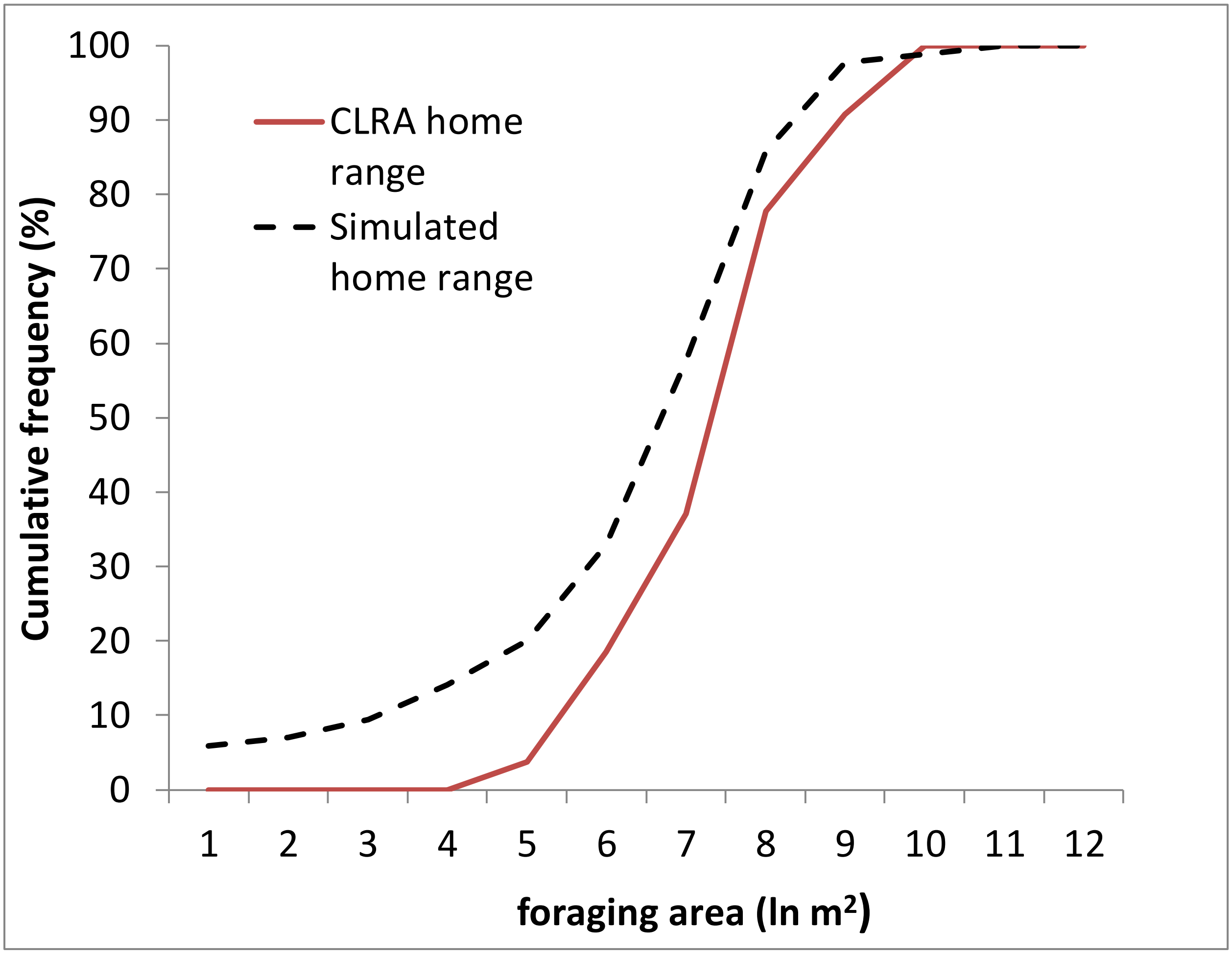

Figure 3.4B. Distributions of natural log transformed foraging areas of observed and simulated home ranges. Observed home ranges generally contained more foraging areas than simulated.

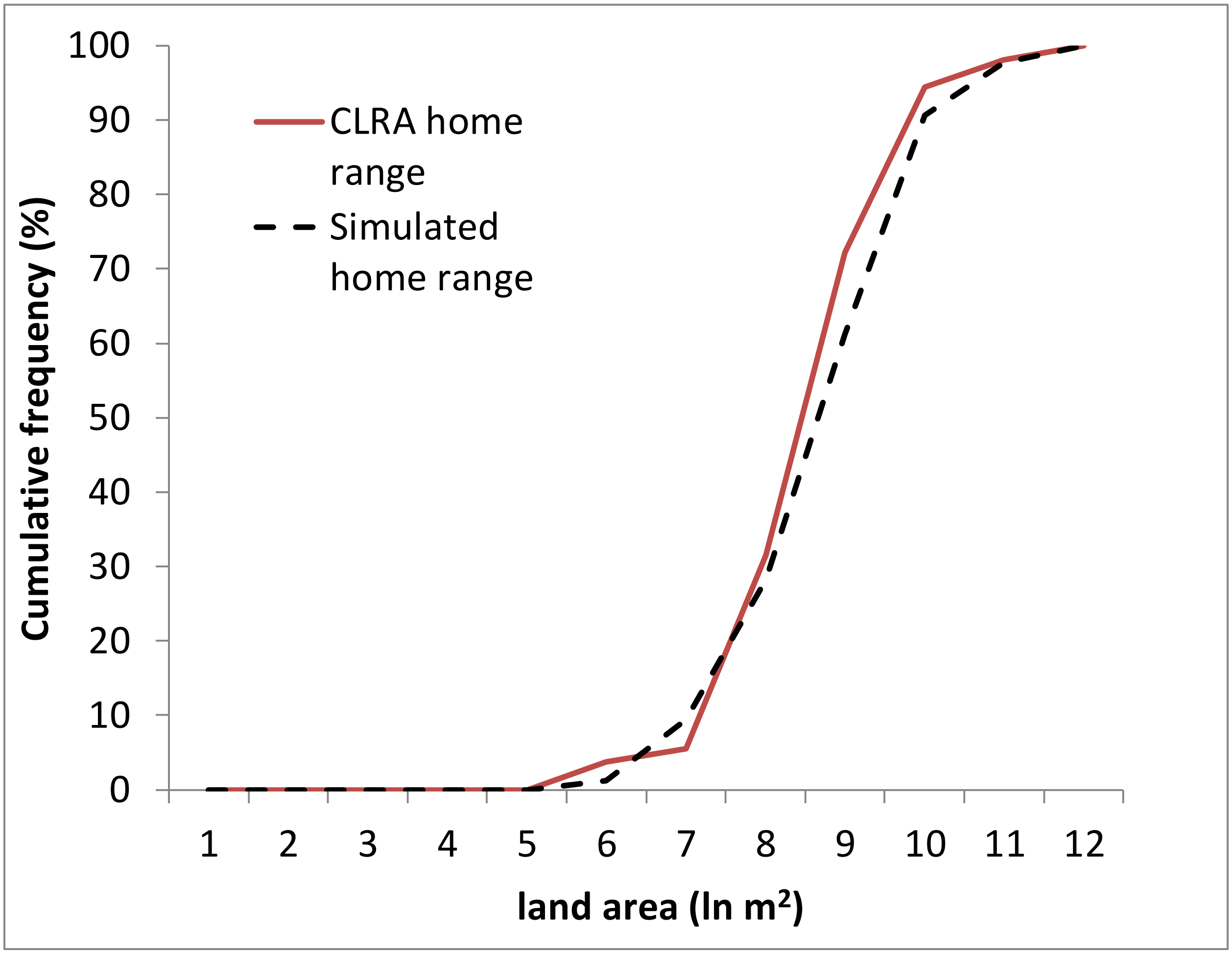

Figure 3.4C. Distributions of natural log transformed land areas for observed and simulated home ranges.

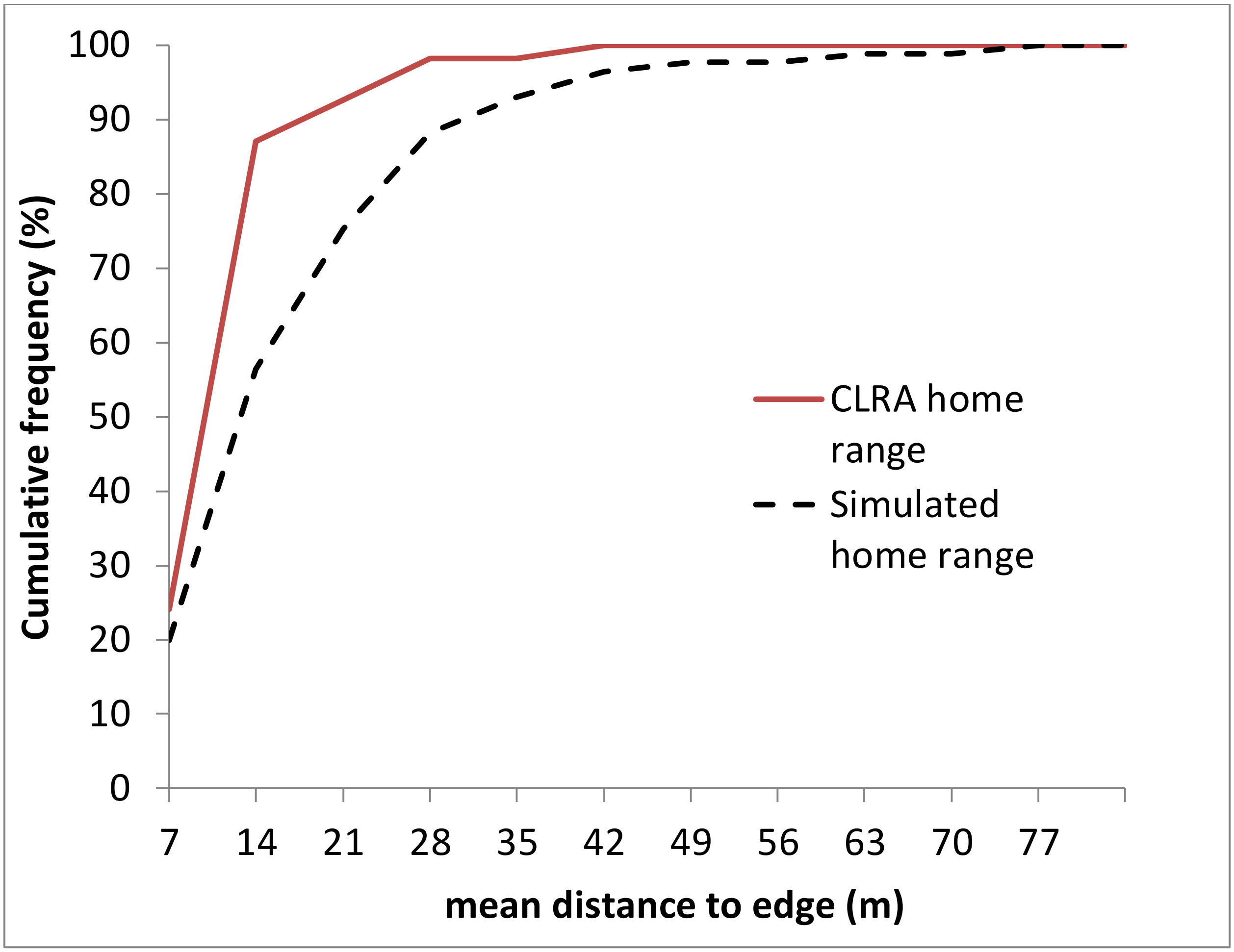

Figure 3.4D. Distributions of mean distance to edge (m) for observed and simulated home ranges. Observed home ranges generally contained a shorter mean distance.

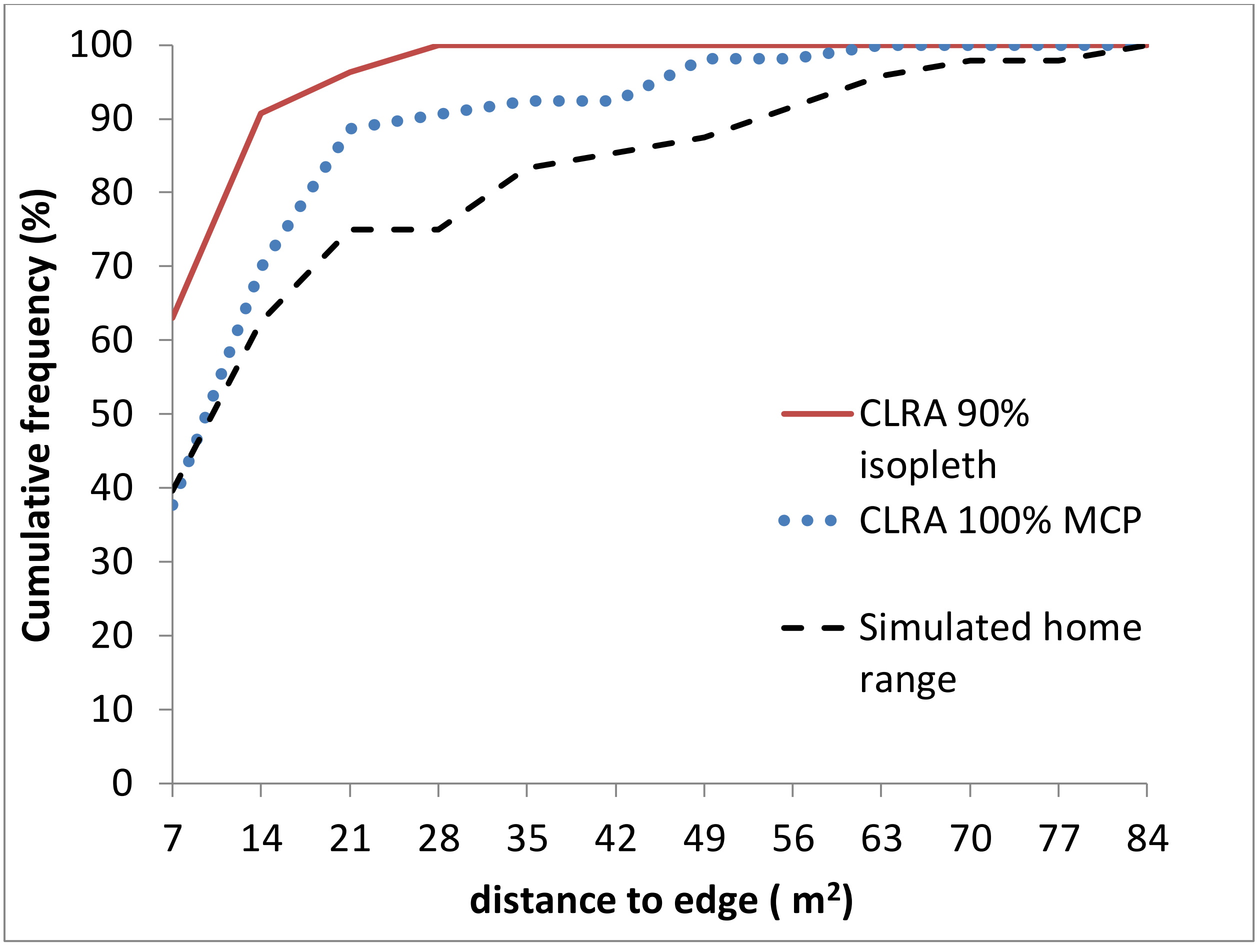

Figure 3.5A. Distance to edge, as measured from random sampling locations within the home range, was typically shorter in observed home ranges. Within an observed home range, mean distance to edge was shorter in the 90% isopleth than outside the 90% isopleth but within the outer boundary (100% MCP).

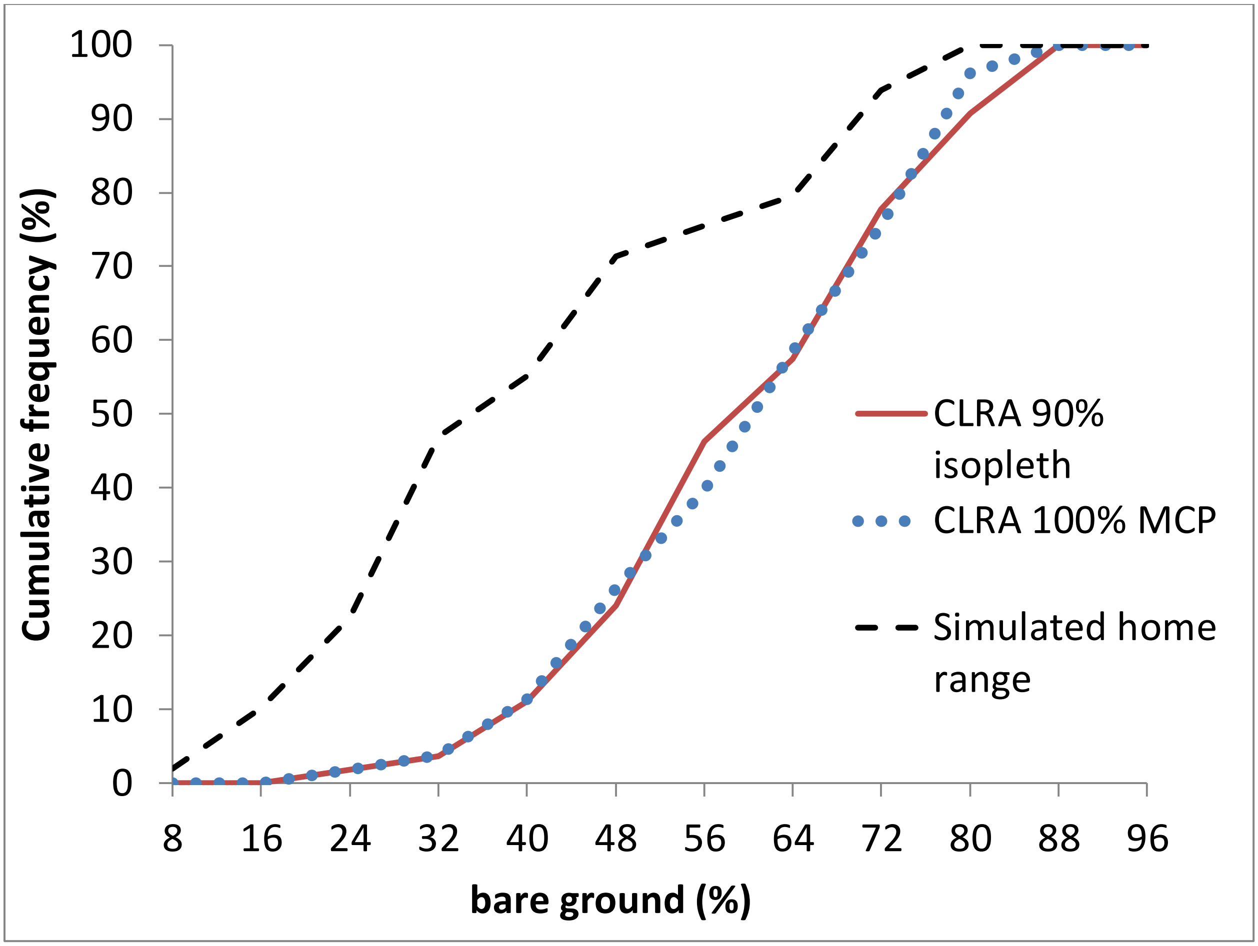

Figure 3.5B. Distributions showing percent bare ground in observed and simulated home ranges. Observed home ranges typically had more bare ground than simulated sites, but there was no difference in this metric within an observed home range.

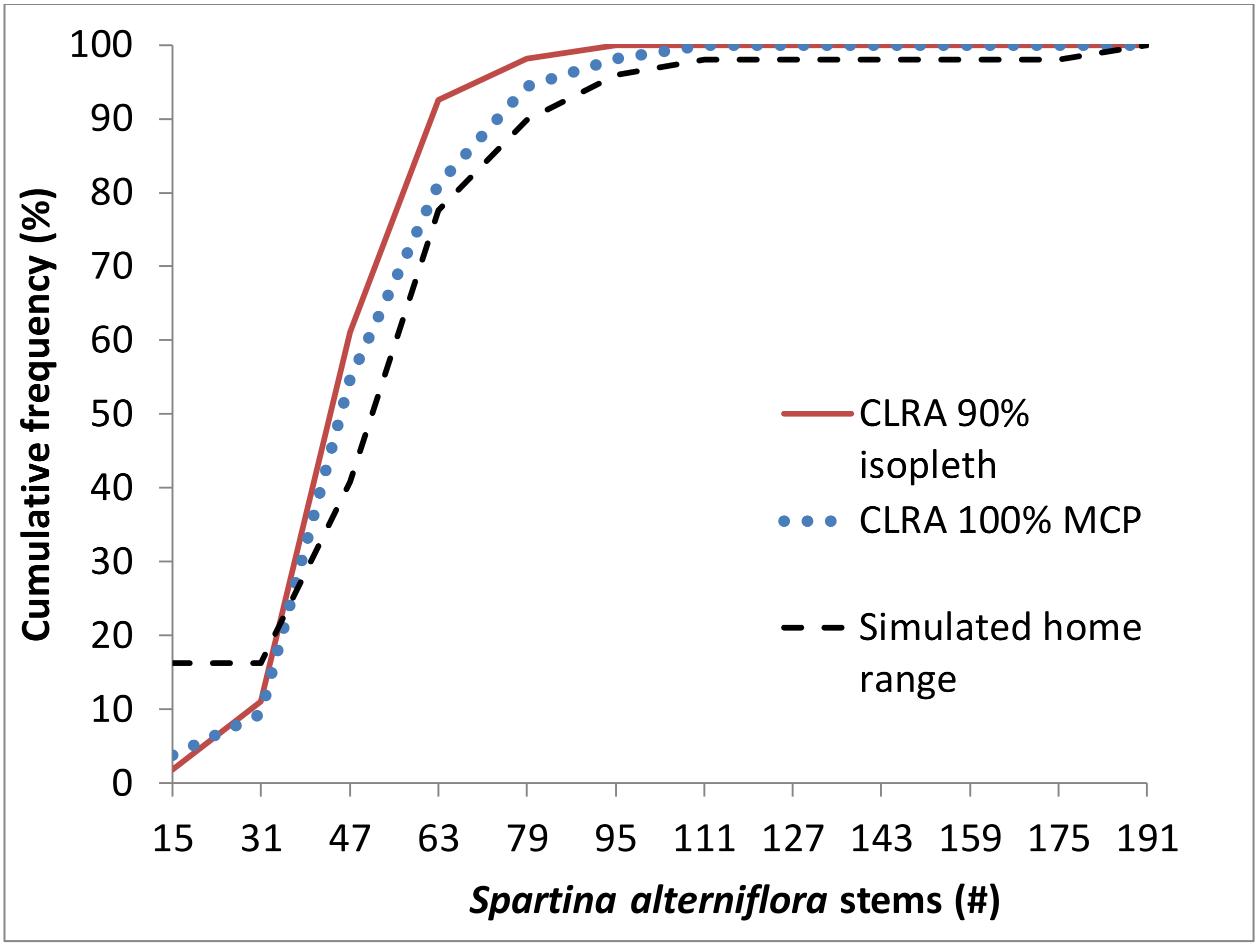

Figure 3.5C. Distributions of stem density, measured at random sampling locations, within observed and simulated home ranges. Stem density was typically slightly lower in observed sites. Within an observed home range, stem density was slightly lower in the 90% isopleth than outside the 90% isopleth but within the outer boundary (100% MCP).

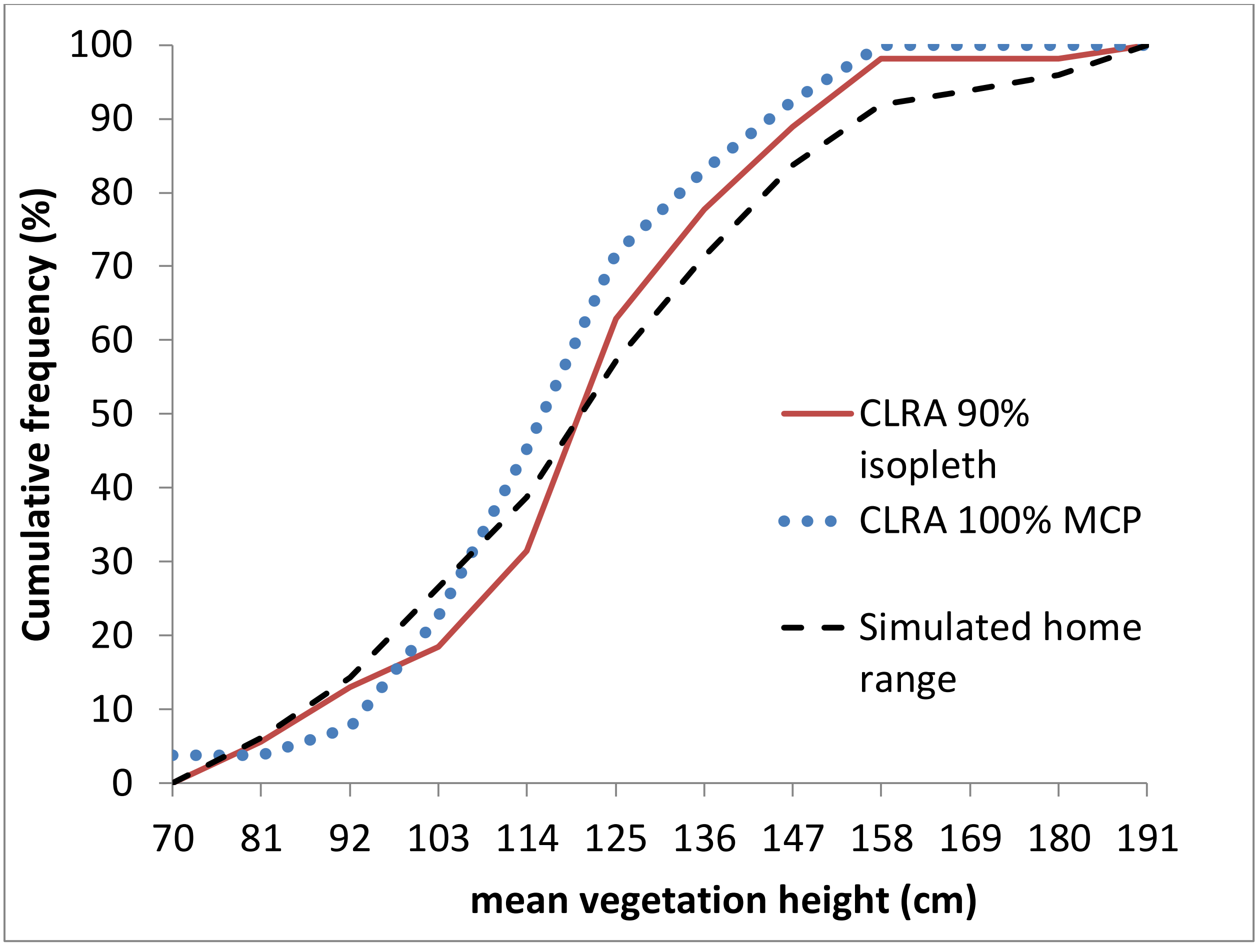

Figure 3.5D. Distributions of mean vegetation height, measured at random sampling locations, within observed and simulated home ranges. Within an observed home range, vegetation was typically taller in the 90% isopleth than outside the 90% isopleth but within the outer boundary (100% MCP).

CHAPTER 4

NEST SITE CHOICE AND REPRODUCTIVE OUTCOMES FOR CLAPPER RAILS (*RALLUS LONGIROSTRIS*) IN SOUTH CAROLINA[1]

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[1] Ricketts, C. E., J. Hepinstall-Cymerman, W. E. Mills, R. J. Cooper, S. H. Schweitzer, and E. P. Wiggers. To be submitted to *The Auk*.

ABSTRACT

Resident tidal marsh birds must minimize risks from both predation and regular tidal flooding to reproduce successfully. Nest site selection represents a trade-off between conflicting strategies to avoid these two main risk factors. We studied mechanisms for addressing these trade-offs in nest site selection by the clapper rail (*Rallus longirostris*) across two years in South Carolina. At the landscape-scale, rails selected nest sites that experienced significantly lower seasonal maximum tides compared to randomly available sites. At the local-scale, rails chose nest sites with significantly taller and denser vegetation compared to paired sites, but these factors did not increase nest survival probability. Nest survival probabilities decreased as distance to non-marsh habitat (e.g., pine woods) decreased. Thus, despite rails' apparent ability to select sites minimizing flooding risk, they appeared not to select for a proximity to non-marsh habitat (i.e., a nest predator source); even though increased proximity reduced overall nest survival probabilities.

Key words: clapper rail, nest success, nest site selection, logistic exposure

INTRODUCTION

A common research objective in developing management strategies is to identify "high quality habitat"—where populations persist and growth rate is positive—for a particular species. In this context, habitats historically were labeled high quality if they were deemed to include sufficient resources for the species under investigation, but without verification of population parameters (Van Horne 1983). Currently, researchers usually assess habitat quality using demographic metrics because of the inherent relationships among an individual's fitness, its habitat, and population level consequences (Fretwell and Lucas 1970, Johnson 2007). Studies of an individual's condition or of habitat selection are other methods to distinguish high and low quality habitats. Combining more than one method provides greater insights into the system in question (Johnson 2007).

Habitat selection is a hierarchical process: first-order selection originates at a broad scale and encompasses a species' geographic range; second-order selection refers to a choice of home range (e.g., see Chapter 3); third-order selection refers to differential use of habitat within a home range (e.g., choice of nest or foraging site); and fourth-order selection refers to, for example, choice of prey item at a foraging site (Johnson 1980). Broad scale choices do constrain the selection occurring at finer scales but spatially and temporally dependent cues present at multiple scales may influence individuals' selections (Orians and Wittenberger 1991, Chalfoun and Martin 2007). Earlier work focused on the one scale of analysis believed most relevant to the organism (reviewed in Wiens 1989). However, researchers analyzing selection processes at multiple scales may identify important variables otherwise overlooked (Martinez et al. 2003, Whittingham et al. 2005, Bakermans and Rodewald 2006), develop models accounting for more variability than a single-scale counterpart (Piorecky and Prescott 2006), and clarify instances where choices at one scale appear maladaptive (Chalfoun and Martin 2007). The latter example demonstrates that using multiple methods and scales of analysis results in a more complete ecological understanding of quality habitat for a species.

Projected changes to coastal areas from sea level rise (Erwin et al. 2006, van de Pol et al. 2010), along with ongoing threats from invasive plants, fragmentation, pollution, siltation, dredging, and channelization (Cooper 2007, Cumbee et al. 2008) require implementation of sound management actions to achieve appropriate conservation goals. Wetland-associated species have already been affected by the more than 1.2 million hectares of U.S. wetlands converted to other uses between the mid–1970s and 1997 (Dahl and Johnson 1991, Dahl 2000, Dahl 2006, Cooper 2007). Mitigation and restoration efforts increased the overall amount of wetland area between 1998 and 2004, but total hectares of both freshwater and brackish (i.e., estuarine) tidal marsh declined slightly within that same time period (Dahl 2006). Although wetland loss is often mitigated by creation of anthropogenic wetlands, including marshes, it is unclear if these habitats are capable of sustaining marsh obligate species (Boyer and Zedler 1998, Melvin and Webb 1998, Desrochers et al. 2008). Remaining natural marsh habitat becomes increasingly important to populations that use these landscapes (Eddleman et al. 1988).

Tidal marsh systems challenge the survival and reproductive efforts of its residents in ways foreign to their non-tidal marsh relatives (Greenberg et al. 2006a). To survive, animals have physiologically adapted to increased water salinity (e.g., Olson 1997), to food sources dominated by invertebrates rather than plants (Grenier and Greenberg 2006), and to foraging sites often exposed to aerial predators (Greenberg et al. 2006a). Thus far, avian species dominate much of the research into animals' reproductive strategies in tidal marshes. Birds must avoid nest depredation in an area with reduced structure and cover compared to terrestrial landscapes and avoid nest destruction by regular tidal flooding to reproduce successfully (Storey et al. 1988, Greenberg et al. 2006b, Reinert 2006, Rush et al. 2010).

Reproductive choices in the tidal marsh often involve trade-offs between strategies to avoid these two primary threats, the results (i.e., nest success or failure) of which manifest in evolutionary adaptations such as short re-nesting intervals, synchronous nesting, and the use of environmental cues to select nest sites (Storey et al. 1988, Reinert 2006, Shriver et al. 2007). Nest site selection is a reproductive choice that typifies these trade-offs. For example, tall forms of one of the most common nest substrates, the often dominant smooth cordgrass (*Spartina alterniflora*), grow at water's edge while short forms grow further inland. The tall forms provide more cover from predation for nesting species but leave those nests more vulnerable to flooding. Conversely, the location of the short form grasses may reduce risk from flooding, but increases nest exposure to predators.

The clapper rail (*Rallus longirostris*), a brackish-saline tidal marsh obligate gamebird, uses smooth cordgrass as a primary nest substrate in coastal South Carolina. The natural history, including basic breeding biology and nest characteristics, of eastern clapper rails has been well documented, especially for the Carolinas and Georgia (e.g., Oney 1954, Adams and Quay 1958, Blandin 1963, Meanley 1985, Gaines et al. 2003), but only one study described nest success linked with vegetation types (Kozicky and Schmidt 1949). Other reports of reproductive output have described solely, or in combination, mean clutch size, number of chicks hatched, nest density, seasonal re-nesting attempts, and apparent success rates (e.g., Stewart 1951, Blandin 1963, Mangold 1974). However, the primary objective of these studies was to develop population indices. Thus, estimates both of population numbers and of basic demographic parameters are non–existent (MSUGBSTF 2009) mainly because historical data are lacking

(Cooper 2007). The data collected are also insufficient to quantify retroactively the relationship between habitat and reproductive outcomes (i.e., assess habitat quality), although a recent comparative study of two marshes of differing salinities in Mississippi linked demographic parameters with habitat characteristics (Rush et al. 2010).

The general goal for my research was to elucidate the characteristics of high quality breeding habitat for clapper rails by combining analyses of clapper rail nest site selection and nest survival. Correspondence between characteristics of selected nest sites and successful nests would indicate higher quality habitat for this species because individual choices translate into positive consequences for the population. The inclusion of environmental characteristics at multiple scales may explain observed mismatches between characteristics of selected sites and reproductive outcomes.

The first objective of this chapter was to examine clapper rail nest site selection at two scales. Avian species can prospect an area looking for signs of reproductive success and employ that social information as a basis for their own future nest site choice (Doligez et al. 2002, Betts et al. 2008). They may also survey locations for appropriate environmental conditions before choosing a site (Storey et al. 2008). Southern Atlantic Coast rails are residents in the tidal marsh and so may be able to use year-round social and/or environmental information to aide in nest site selection. I focused on the effects of environmental characteristics at two scales: landscape (within study area) and local (within home range), in assessing clapper rail nest site (or third-order) selection (Johnson 1980) to investigate how rails mitigate flooding and predation risk at these scales. I compared landscape-scale characteristics of clapper rails' chosen nest sites to those at randomly available sites within the entire study area (hereafter, "randomly available sites"). I compared local-scale characteristics of each chosen nest sites to those at a locally available site paired with each nest (hereafter “paired site”). I based my hypotheses on the key habitat features reported in earlier works. At a landscape scale, I hypothesized that nest sites would be located farther from sources of terrestrial predators and that nest sites would experience lower seasonal maximum high tides compared to randomly available sites within the study area. At a local scale, I hypothesized that nest sites would be in taller, denser vegetation and closer to water’s edge compared to paired local sites. These factors would also be the most important predictors of a nest site versus a local site.

My second objective was to determine which environmental characteristics contributed to successful nests and if they corresponded to rail nest site selection. Numerous studies have reported the general habitat types associated with rail nests, but not reproductive outcomes of these associations (e.g., Lewis and Garrison 1983). I modeled the relationship between nest success and habitat characteristics based on biological hypotheses about which environmental variables were most important. I hypothesized that two local-scale variables, vegetation height and density, along with a single landscape-scale variable, maximum tidal height, would best predict nest success. These factors would also be the most important predictors of daily nest survival.

I also calculated daily survival rate (DSR) for Atlantic Coast clapper rail nests. In addition, I documented the relationship between clutch size and initiation date, causes of nest failure, and number of chicks hatched.

STUDY AREA

The Ashepoo-Combahee-Edisto (ACE) Basin in southern coastal South Carolina is largely rural (Coastal Services Center 2000) and provides opportunities to conserve and restore critical habitat for marsh bird species (Tufford 2005). Part of the Basin is within the National Oceanic and Atmospheric Administration’s National Estuarine Research Reserve System and contains land protected through the cooperation of State, Federal, private, and nonprofit interests (Coastal Services Center 2000).

In this study I focused on an approximately 2,300 ha portion of tidal marsh along the Combahee River and Wimbee Creek within the ACE Basin (Figure 4.1). The study area was approximately 8 km north to south and covered a range of salinity values (W. E. Mills, personal communication). The Combahee River Bridge on U.S. highway 17 delineates the legal transition from salt to fresh water and the highway formed the northern boundary of the study area. The Wimbee Creek Landing was the southern boundary. The western boundary abutted the marsh edge primarily along the Nemours Plantation Wildlife Foundation property line while other private plantation property lines adjacent to the Combahee River formed the eastern boundary.

Smooth cordgrass dominates the marsh of these two connected water bodies. Black needlerush (*Juncus roemerianus*) grows in largely homogeneous patches mainly in the northern portion of the study area and also in higher elevations throughout. Saltmarsh bulrush (*Schoenoplectus robustus*), big cordgrass (*Spartina cynosuroides*), and soft-stemmed bulrush (*Schoenoplectus tabernaemontani*) are interspersed with smooth cordgrass, mainly in the northern portion of the study area while saltmarsh aster (*Symphyotrichum tenuifolium*) is interspersed with smooth cordgrass throughout the study area (personal observation).

A fundamental attribute of the study area’s smooth cordgrass marshes is that grasses generally grow taller and denser nearer the edges of river channels and gutter creeks compared to interior marsh locations farther from these water sources. Interior grasses are subject to regular higher salinity during low tide periods when water can be absent or levels very low as evaporation concentrates the salt. Despite the ability of smooth cordgrass to excrete excess salt, growth is stunted compared to forms nearer the edge of waterways where flow and volume are greater.

In coastal South Carolina, tides are semidiurnal with a tidal extreme (i.e., high tide or low tide) occurring approximately every 6 hours. In a 24-hour period there are 2 high tides (and 2 low tides) but they are not of equal height and are thus termed “higher high water” and “lower high water.” Similarly, the low tides are referred to as “higher low water” and “lower low water.” The maximum tidal height within a 24-hour period is the higher high (HH) water. Because tidal flooding is known to cause rail nest failure, I used data for HH water in my analyses. Diurnal tidal range is approximately 2.3 m for my study area.

METHODS

Nest searching and monitoring

I searched for nests from mid-March to August of 2009 and 2010 using three different strategies. I outfitted some clapper rails in the study area with radio-transmitters for a related study (see Chapter 3). To document as many nesting attempts of rails with radio-transmitters as possible, I focused searches in areas where I detected marked birds on multiple days. I also performed systematic searches of tidal marsh within the study area to locate nests of rails with and without radio-transmitters. Third, during high tide, I searched by boat for nests along marsh edges that were often inaccessible (by boat or on foot) during low tide. I found nests in building, laying, and incubation phases. I marked the location of each active nest with a handheld GPS unit (Garmin Corporation, Olathe, Kansas). I defined active nests as those with at least one viable egg present. If I found a nest in the building phase it would not be identified as an active nest until the first egg was laid. If I found a nest in the laying or incubation phase I floated eggs in the clutch to estimate nest age (Rush et al. 2007) and predict hatch date. The mean observation interval, or time between visits to the nest, was two days (standard deviation, SD: 0.74 days; range: 1 to 5 days) during laying and early-mid incubation phases. At each visit I collected data on the number of adults present, identity of adults (i.e., bird with radio-transmitter or not), number of eggs present, and if applicable, evidence of predation or evidence of nest destruction by a tidal event. Additionally, I recorded the date and time of the nest visit. As the projected hatching date approached (≤ 1 week) I visited a nest every day (with some exceptions, e.g., thunderstorms, low tide inaccessibility) until the nest hatched or failed. When a nest hatched, I documented the number of chicks present and if applicable, the number of eggs remaining. I revisited a newly hatched nest in subsequent days to determine if remaining eggs hatched. Because clapper rails are precocial (i.e., no nestling phase), I considered a nest successful if at least one egg hatched.

Landscape-scale environmental variables

Biotic and abiotic landscape-level factors could influence rails' nest site selection. At this scale I compared characteristics of rails' chosen nest sites with characteristics at 56 randomly available sites within the study area obtained through a systematic random sampling scheme. In 2009, I found no nests at these randomly available sites but they were not checked in 2010. Rails may select nest sites farther from non-marsh habitat because of a reduced threat from terrestrial predators and thus an increased probability of nest success. Avian nest predation is possible but I assumed an equal probability of this event regardless of landscape position. In a GIS, I digitized sources of terrestrial predators from aerial photographs of the study site (Figure 4.2). I defined these sources as all non-marsh habitats contiguous to or within the study area which mainly consisted of the study area edges (e.g., where the marsh met the pine woods of a plantation) and the tree islands scattered throughout the marsh itself. I used this polygon layer, along with a digital hydrography layer of main stream channels, to create a 5 m grid cell cost-distance surface raster. This raster represented the effective distance a predator must travel to find each nest site and each randomly available site. I assumed that a terrestrial predator could access sites close to non-marsh habitat more easily than those sites separated from non-marsh habitat by main waterways. The effective distance calculation weighted main river channels by assigning a high value (i.e., cost) to those cells; marsh land cells were assigned a low value. The cost-distance from a source to a site equaled the lowest possible sum of cell values. I also used the cost-distance values calculated for nest sites as an explanatory variable in the analysis of nest success (Table 4.1).

The highest tide experienced by a nest site or randomly available site depends not only on the distance between the site and the vegetation edge, but also the site's overall location in the marsh. The National Oceanic and Atmospheric Administration/National Ocean Service/Center for Operational Oceanographic Products and Services' (hereafter, NOAA) station located at Ft. Pulaski, Georgia, predicts tides for the study area. NOAA also publishes verified tidal data. I obtained this verified data for part of 2008 (August through December), and all of 2009 and 2010. I recalculated the heights and times for my study site based on NOAA published correction factors for the U.S. 17 bridge at the Combahee River (the northern boundary) and for Wimbee Creek Landing (the southern boundary). Because my study site is approximately 8 km long, the daily HH water fluctuated by as much as 2.22 m between the northern and southern boundaries during the study period. I created a daily adjustment factor to estimate site-specific HH water levels by using a simple linear relationship. I used the northern boundary HH water value for each day as a reference and calculated the increase in water height for each meter (i.e., UTM Northing) southward, ending at the Wimbee Creek Landing. In the nest site selection analysis, I used the seasonal maximum HH water experienced by each nest site and randomly available site during the pre-breeding and breeding seasons as a factor. The seasonal maximum HH water value served as an indicator of flooding potential for a site and rails may use this environmental cue in the selection process. I defined the pre-breeding season as August 1 to February 28, 2009, and 2010, and the breeding season as March 1, 2009 to July 31, 2009, and 2010. In the nest success analysis, I used the maximum HH water for each observation interval of an active nest as a factor (Table 4.1).

Local-scale environmental variables

Previous work (e.g., Lewis and Garrison 1983, McGregor 2007) has suggested that local-scale variables such as vegetation height and distance to flowing water are predictors of quality rail habitat. In a nest site selection context, taller grasses, higher stem densities, and a lower percentage of bare ground provide more cover from nest predators although, generally, these vegetation characteristics occur closest to water's edge where tidal flooding can destroy nests. To investigate how rails address this trade-off in site selection, I measured vegetation characteristics at the nest site within a 0.25 m^2 (0.5 m by 0.5 m) frame centered on the nest once it was no longer active. I recorded the species present, stem density (the number of stems of each species per 0.25 m^2), % cover of each species, % bare ground, dominant vegetation height (the mean height of vegetation recorded in each of the four cardinal directions), and the distance to the nearest flowing water (represented as vegetation edge) from the center of the frame (after Rush et al. 2010). I measured the same set of habitat characteristics within a 0.25 m^2 sampling frame at a site paired with each nest. These paired sites were located at a random distance ($\leq$ 50 m) and bearing from each nest. In both years, I found no nests at the local sites. I included these local-scale variables measured at the nest site as factors in the nest success analyses (Table 4.1).

Statistical analysis

For both 2009 and 2010 landscape level nest site selection, I used 3 t-tests to compare means of the environmental variables (maximum HH water during pre-breeding and breeding seasons; distance to non-marsh habitat) between chosen nest sites and randomly available sites.

To evaluate local nest site selection by clapper rails, I used conditional logistic regression which compared matched binary (i.e., case-control) response variables based on included covariates (Hosmer and Lemeshow 2000). I included covariates only where all pairwise correlations resulted in $r^2 < 0.5$ (Fielding and Haworth 1995). Cases (nest sites) were matched with controls (paired sites) and each match represented a single stratum. Parameter estimates for each stratum were considered nuisance outcomes and thus the emphasis was on the overall probability of covariates representing a case versus a control. I conducted this analysis for each nest site and its paired site for which I had measured a full suite of environmental variables (98 strata).

I developed eight candidate models describing biological hypotheses explaining potential strategies employed by clapper rails when selecting a nest site (Table 4.2). I used an information theoretic approach to evaluate support for candidate models based on the data (Burnham and Anderson 2002). I ranked candidate models according to a second order Akaike Information Criterion, AIC_c (Akaike 1973, Hurvich and Tsai 1989). The best approximating, or most plausible, model given the data had the lowest AIC_c value and, by default, the highest Akaike weight of evidence, w_i. The confidence set of models included all models where $\Delta AIC_c \leq 2$.

I created a composite model using model-averaged parameter estimates for those parameters present in the confidence set. I weighted each parameter estimate by the w_i from every candidate model in which it appeared and then summed these weighted values for the model-averaged estimate (Burnham and Anderson 2002). I also calculated 95% confidence intervals for the model-averaged parameter estimates. I based all inferences on the composite model.

To aid in interpretation and comparison of each predictor variable's effect on nest site selection, I computed scaled odds ratios for parameter estimates and confidence intervals of the composite model (Hosmer and Lemeshow 2000). I calculated scaled odds-ratios for two reasons. First, scaling the odds-ratios facilitates a comparison of effect on the response variable among parameters with different units. Second, a scaled odds-ratio for a parameter estimate can reflect a more biologically meaningful change in the response variable. An unscaled odds-ratio describes the impact of a one-unit change on the response variable. In this system, for example, it is more realistic biologically to consider the scaled effect of a 10 cm change (versus a 1 cm change) in vegetation height on the probability of nest presence. I calculated importance weights—the summed Akaike weights across all candidate models containing a specific parameter—for each covariate in the composite model. Importance weights provided insight into the most influential parameter(s) on the response variable given the data and the candidate models.

I used the logistic exposure method to estimate the probability of daily nest survival. This form of logistic regression was designed to address the inherent assumptions and biases of previous daily nest survival estimation methods (Shaffer 2004). The logistic exposure method assumed that each nest's probability of survival was independent of other nests, a trait shared by other analysis techniques. However, daily survival probabilities were not assumed homogeneous across nest-days and instead could vary when values of the covariates vary and with observation interval length (Shaffer 2004). The latter was reflected in the logit link which contained the exponent $1/t$ (eqn. 1). The denominator, t, in the exponent was the number of days in an observation interval and Θ was the probability of success (i.e., survival) during that same period.

$$g(\Theta) = \ln\left(\frac{\theta^{\frac{1}{t}}}{1-\theta^{\frac{1}{t}}}\right) \qquad \text{(eqn. 1)}$$

I developed 17 candidate models based on biological hypotheses to describe the daily survival of clapper rail nests (n = 95: 2009, n = 34; 2010, n = 61) (Table 4.3). I used covariates only where all pairwise correlations resulted in $r^2 < 0.5$ (Fielding and Haworth 1995). I included both a global model with all covariates and a null model assuming constant survival. In the models where maximum HH water is a covariate, I used both a linear and quadratic effect. The quadratic effect accounted for the cyclical nature of tides during an individual nesting period (approximately 29 days: 8 days for laying and 21 days for incubation). During late June 2009, a perigean spring tide exacerbated by the East Coast Sea Level Anomaly 2009 (Sweet et al. 2009) occurred where maximum HH water was as much as 0.6 m above the prediction. Because this event directly impacted the survival of multiple active nests, I added interaction terms between year and local scale factors (distance to vegetation edge and mean grass height) to several models. Initial evaluation showed the interactions were not significant (i.e., confidence intervals included 0) and so were dropped from the final candidate set of models. I also conducted logistic exposure analysis for each year's data separately, but ultimately used the pooled data for inferences.

To evaluate support for candidate models based on the data (Burnham and Anderson 2002), and use AIC_c (Akaike 1973, Hurvich and Tsai 1989), I calculated an effective sample size, *n-eff*, after Rotella et al. (2004). The effective sample size, *n-eff*, ensures that the small sample size adjustment is correct when calculating AIC_c. The value for *n-eff* equaled the total number of days each nest was alive in each observation interval, summed across all observation intervals for each nest if it was successful. If the nest failed, the final interval was assigned a 1 and was added to the previous intervals' sum (Rotella et al. 2004). The best approximating, or most plausible, model had the lowest AIC_c value and, by default, the highest Akaike weight of evidence, w_i. The confidence set of models included all models where $\Delta\ AIC_c \leq 2$.

I created a composite model, as described above, using model-averaged parameter estimates for those parameters present in the confidence set. I based all inferences on the composite model and I used scaled odds-ratios and importance weights to aid in interpretation of modeling results.

RESULTS

General results

I found and monitored 132 active clapper rail nests (2009, n = 55; 2010, n = 77). Although search attempts included sections of marsh dominated by black needlerush and sections with a mix of smooth cordgrass and saltmarsh bulrush, every nest found was constructed in smooth cordgrass. Saltmarsh aster, black needlerush and saltmarsh bulrush were present at only 6.7% (7/104) of the nest sites measured (i.e., within the 0.25 m^2 sampling frame), and were not dominant at these sites.

Mean clutch size was 7.54 (SD = 1.90; range: 3 to 12) eggs per nest for nests with a known full clutch (n = 95), which did not differ across years (Table 4.4). Both males and females incubated nests. I estimated a minimum mean incubation length of 20.41 days and maximum mean incubation length of 21.47 days for nests with known initiation date and known hatch date (2009, n = 5; 2010, n = 12). Thus, I used 21 days as the incubation length to back-calculate initiation date from the hatch date for those nests I discovered with an already full clutch. As the breeding season progressed in both years, clutch size decreased (Figure 4.3). A total of 300 chicks were produced from 48 nests in 2009 and 2010. Mean number of chicks hatched per nest was 6.25 (SD = 2.07; range: 1 to 12) and did not differ between years (Table 4.5).

I assigned a definitive fate (i.e., success or failure) to 121 nests (2009, n = 48; 2010, n = 73). I determined that 39 nests failed due to predation based on evidence observed at the nest site. This evidence was rodent droppings, most likely from the marsh rice rat (*Oryzomys palustris*) (n = 6); large eggshell fragments present at a date when hatching would be impossible (i.e., too early in incubation) (n = 26); or tracks and eggshells present (n = 4). All tracks observed were of raccoon (*Procyon lotor*). Tidal flooding washed away 10 nests. An additional 27 nests failed but I was unable to determine a cause.

Nest site selection

At the landscape scale, the data supported one out of two hypotheses. Nest sites experienced lower maximum HH water during both pre-breeding seasons than did the randomly available sites (2009: $t = 3.89$, $df = 89$, $p < 0.0001$; 2010: $t = 3.94$, $df = 117$, $p < 0.0001$). During breeding seasons of both years this relationship was the same (2009: $t = 3.86$, $df = 89$, $p = 0.0001$; 2010: $t = 5.37$, $df = 117$, $p < 0.0001$) (Table 4.6). Contrary to my prediction there was no difference within (2009: $t = 0.87$, $df = 89$, $p = 0.19$; 2010: $t = 1.31$, $df = 117$, $p = 0.10$) or across ($t = 1.42$, $df = 152$, $p = 0.08$) years between the nest sites and randomly available sites in the distance to sources of terrestrial predators.

At the local scale, the most plausible model explaining nest site selection was the predator avoidance model (Table 4.7). This model was 2.8 times more likely than the next best approximating model, the global model (Table 4.7). These two models comprised the confidence set of models. Because the global model was included, I calculated model-averaged estimates of all parameters for the composite model of local scale nest site selection (Table 4.8).

The percentage of bare ground at a site had a negative relationship with nest presence. For every 10% increase in the amount of bare ground, nest presence was almost 2 times (1/0.514) less likely (Table 4.8). Vegetation density (# stems/0.25 m^2) was positively related to nest presence: for every 10-stem increase in density a nest was 1.7 times more likely (Table 4.8). Importance weights showed that percentage of bare ground was a slightly more plausible (1.14 times that of density) explanation for nest presence at a site (Table 4.8). Mean grass height appeared to be positively related to nest presence as the scaled odds-ratio indicated a trend toward increased probability of a nest with each 20 cm increase in height. However, the confidence interval for the scaled odds-ratio of this parameter included one, thus the exact nature of the relationship was inconclusive. Similarly, the relationship of distance to edge with nest presence was inconclusive (Table 4.8).

Modeling results strongly supported one aspect of my hypothesis—that nests would be located in denser vegetation than paired sites. There was some support for the prediction that nests would be located in taller vegetation and minimal support for the prediction that nests would be closer to an edge.

Nest survival

The most plausible model explaining clapper rail nest survival was the predator-tide model (Table 4.9). This model was 2.3 times more likely than the next best approximating model, the predator-tide-date model (Table 4.9). These two models comprised the confidence set of models and were combined into the composite model of nest survival which included cost-distance to predator source, Julian date, year, and the quadratic and linear maximum HH water terms (Table 4.10).

The linear and quadratic terms for maximum HH water had a strong relationship with nest survival and confidence intervals around each odds-ratio estimate excluded 1 (Table 4.10). An odds-ratio > 1 for the linear term combined with an odds-ratio < 1 for the quadratic term corresponded to a unimodal response curve with nest survival increasing up to a threshold value of maximum HH water and then decreasing. The cost-distance to predator sources had a positive relationship with nest survival. For every 500-unit increase in cost-distance, nest survival was 10% more likely (Table 4.10). Importance weights showed that maximum HH water was a slightly more plausible explanation for nest survival (1.08 times more likely) than cost-distance to predator sources (Table 4.10). Study year appeared to have some impact on nest survival: in 2009 survival was 1.59 (1/0.626) times less likely than in 2010, but the confidence interval for this odds-ratio included one so the exact nature of the relationship was inconclusive. The day of the breeding season (i.e., Julian date) appeared to have little effect on nest survival (Table 4.10).

The composite model of DSR for clapper rail nests was thus:

logit ($\widehat{S_\iota}$) = -37.634 + 0.0007(Julian date) + 36.587(max. HH water) – 8.180(max. HH water ^{2}) + 0.0002(predator cost-distance) – 0.468(year)

Mean DSR was 0.972 and mean period survival (DSR^{29}) was 0.435.

I graphed the relationship between DSR and the two parameters of the composite model for which the affect on DSR was clear: cost-distance to predators and maximum HH water. Lower DSR values corresponded to lower observed mean daily HH water and also to observed daily mean HH water above a threshold height of approximately 2.4 m (Figure 4.4). DSR was lower if a nest site was located closer to non-marsh habitat (i.e., a source of terrestrial predators) (Figure 4.4).

The probability of period survival—a nest surviving from initiation date to hatch date—showed a similar pattern to DSR across HH water values, but the range was larger (Figure 4.5). The peak of period survival probability for a nest, regardless of its proximity to non-marsh habitat, occurred when HH water was at an intermediate height of approximately 2.2 m. When HH water was held constant at its minimum observed value (1.62 m), period survival was essentially 0 at all cost-distance measurements (Figure 4.6). At the mean observed HH water height (2.08 m), period survival probability increased from 0.31 to 0.70 as cost-distance increased. Period survival when HH water was held at its maximum (2.65 m) height also increased with cost-distance, but was much less probable than at the mean HH water value (Figure 4.6).

Contrary to my hypothesis, local-scale variables were not the best predictors of daily nest survival. Interannual variability between covariates of successful nests and between covariates of successful versus failed nests confounded the effect of these data in DSR modeling. Local characteristics of successful nest sites differed between 2009 and 2010. Successful nests in 2009 compared to 2010 were farther from an edge and at sites with shorter vegetation and lower stem density (Figure 4.7). The two years were similar only in the amount of bare ground present at successful nest sites (Figure 4.7).

Local characteristics also differed between failed and successful nest sites in 2009 versus 2010 (Figure 4.7), despite no significant differences when success and failures were pooled across years. During 2009 failed nests were twice as close ($\bar{x}$ = 1.85 m ± 0.32 m) to water's edge as successful nests ($\bar{x}$ = 4.30 m ± 0.57 m). Failed nests were at sites with taller grasses than sites with successful nests (failed: $\bar{x}$ = 161.38 cm ± 9.90 cm; successful: $\bar{x}$ = 131.30 cm ± 10.15cm). During 2010, failed nests were 1.7 times farther from water's edge than successful nests (failed:

$\bar{x}$ = 5.24 m ± 0.95 m; successful: $\bar{x}$ = 3.04 m ± 0.42 m), and in shorter grass (failed: $\bar{x}$ = 131.56 cm ± 6.53 cm; successful: $\bar{x}$ = 157.86 cm ± 6.23 cm). Additionally, failed nests had a greater percentage of bare ground present (failed: $\bar{x}$ = 46% ± 3.47%; successful: $\bar{x}$ = 36% ± 3.43%) (Figure 4.7).

In 2009, the mean distance from water's edge of all nests was 2.89 m. In 2010, mean distance increased to 4.18 m (Figure 4.8). This difference was not statistically significant (t = 1.64, df = 91, p = 0.052), but this shift of more than 1 m from 2009 to 2010 may have reflected a local response to the flood tide of 2009. At all nest sites, the percentages of bare ground present and stem density both increased slightly from 2009 to 2010. Mean vegetation height at all nest sites remained essentially unchanged (Figure 4.8).

The logistic exposure analysis run separately for each year highlighted the interannual variability (data not shown). In 2009, there were 5 models with $AIC_c \leq 2$: local, predator-height, constant, date-location, and bare-height. The best supported model was the local model; however, none of the model-averaged parameter estimates for those present in the 5 models conclusively indicated the direction of effect (all confidence intervals included 0). In 2010, 3 models had AIC_c values ≤ 2: tide-height, predator-tide, and predator-tide-date. The top model was the tide-height model. Out of the 3 models, only tide showed a clear effect and it was the same relationship as found in the pooled data analysis.

DISCUSSION

Nest site selection

Clapper rails chose nest sites based primarily on one landscape- and several local-scale factors. Rails clearly selected sites that experienced lower tidal maxima than the randomly available sites across the study area. Because of spatial continuity and temporal predictability, tidal inundation and fluctuation provided a consistent environmental cue which likely facilitated resident clapper rails' assessment of flooding potential from high water levels. Rails tend to congregate in taller grasses or on higher ground during high water periods (Meanley 1985, Zembal and Massey 1987, Mills et al. 2011), and Storey et al. (1988) suggested the birds may later return to build nests in these areas. Vegetative cover, characterized by the amount of bare ground and stem density, provided the best local indicator of a nest site in this study. Nest sites had, on average, less bare ground, higher stem densities, and trended toward taller vegetation compared to paired sites (Table 4.11). In a recent Mississippi study, clapper rails also selected nest sites with higher stem densities and taller vegetation compared to paired sites (Rush et al. 2010).

The data did not support my prediction that, to avoid terrestrial nest predators, rails would select nest sites farther from non-marsh habitat compared to the randomly available sites. At this scale rail nest site selection may have been driven solely by tidal maxima, or, by tidal maxima in combination with unmeasured factor(s) such as food availability or intraspecific competition. At the local scale, modeling results were inconclusive as to the direction of effect for the distance to edge parameter and it was minimally important in predicting nest sites versus paired sites. A similar result was found for this metric in a study in Mississippi (Rush et al. 2010).

Nest survival

In this project, whether from flooding or predation, a majority of nests (62.8%) failed to hatch a single egg, similar to the 58% failure reported in North Carolina (Adams and Quay 1958). Other studies documented much lower figures: in New Jersey, 11.4% (Mangold 1974) and 10.7% (Kozicky and Schmidt 1949); in Mississippi, 21.1% (Rush et al. 2010). Researchers in New Jersey have implicated tidal flooding as the main cause of nest failure (Kozicky and

Schmidt 1949, Mangold 1974), but in southern studies predation accounted for many cases of nest loss (Adams and Quay 1958, Blandin 1965, Meanley 1985). In my study, nest predation was a primary factor in failures with 51.3% (39/76) of nests lost suffering depredation. Only 13.2% (10/76) of nest failures could be directly attributed to flooding. The remaining 27 nest losses were due to an unidentified factor. The causes of failure for the 27 nests lead to a range of possible outcomes: at one extreme, if all 27 were depredated then tidal flooding had a minimal impact on nest survival; at the other extreme, if all 27 were flooded then tidal flooding and nest predation had an essentially equal impact.

Contrary to my prediction, the composite model of clapper rail nest survival contained no local-scale factors. Instead, both landscape-scale factors, maximum HH water and cost-distance to predator sources (i.e., non-marsh habitat), were the best predictors of nest survival. Reviews and meta-analyses of other research have documented that local scale variables were often inadequate in predicting nest success, especially in terms of predation risk (Chalfoun et al. 2002, Stephens et al. 2003). Factors operating at broader scales were instead key features (e.g., proximity to certain habitat types, Kus et al. 2008). Results from this study agree with those earlier findings.

A recent clapper rail study in Mississippi calculated a DSR = 0.99 at an estuarine site and a DSR = 0.98 at a polyhaline site (Rush et al. 2010). In this coastal South Carolina study, DSR = 0.972. Based on the composite model, peak period survival probability occurred when maximum HH water values equaled 2.2 m (Figure 4.5). Above this threshold, flooding was the greatest threat to nest survival. Below this threshold, terrestrial nest predators posed the most danger. Period survival decreased with increased nest site proximity to non-marsh habitat, at all but the most extreme water heights where survival probabilities approached zero (Figure 4.5).

At the mean HH water level observed, 2.08 m, period survival increased by 100% from the closest distance to non-marsh habitat to the farthest (Figure 4.6). HH water heights would not remain static for an entire nesting period, but for a theoretical comparison, the lowest (1.62 m) and highest (2.65 m) HH water heights observed are also shown. If HH water levels remained at a minimum level, survival was extremely unlikely at any distance, suggesting that higher water serves as a nest protector. At the maximum level, the effect of tidal flooding clearly depressed survival probabilities from the mean HH water level.

Terrestrial nest predator mobility is a probable explanation for the relationship between the two best predictors (water height and distance to non-marsh habitat) and nest survival. The raccoon was a documented clapper rail nest predator in this project and others (Adams and Quay 1958, Meanley 1985). In bottomland hardwoods, freshwater marshes, and areas where riparian zones were interspersed with other habitats (e.g., grasslands) raccoons used waterways and edges as travel corridors (Urban 1970, Cooper at al. 1999, Newbury and Nelson 2007). Raccoon foraging was opportunistic with no detectable search pattern during travel to reach adjacent wetlands or streams (Newbury and Nelson 2007), resulting in a random, i.e., unpredictable, nest predation process at fine scales (*sensu* Cooper et al. 1999). In one freshwater marsh study, radio-marked raccoons had home ranges between 16 and 49 ha, could cover as much as 32 ha in one night, and travel 162 m per hour (Urban 1970). Increasing travel distances did not deter raccoon visits to nests in another freshwater marsh, but visits decreased greatly at water depths > 40 cm (Picman et al. 1993). Greater success for artificial waterfowl nests corresponded to deeper water in a freshwater marsh where mammalian nest predators, including raccoons, were dominant (Jobin and Picman 1997). Wood duck nest success also increased during a period of bottomland hardwood flooding (Nielsen and Gates 2007). However, raccoons did exploit drying conditions to access previously unreachable nests (Coulter and Bryan, Jr. 1995).

Unlike the tidal marsh, these studies referenced above occurred where water level fluctuations were gradual, changing over an entire season, or were characterized by a pulse (i.e., flood event) followed by a slower drawdown. Nevertheless, it is reasonable to believe raccoons present in my study area behaved similarly in response to daily water level fluctuations. Thus, several implications are evident. First, the likelihood that raccoons depredated a nest encountered as they moved along tidal creeks was high. Given that clapper rails placed their nests, on average, 3.7 m (Table 4.11) from water's edge, nests closer than average to these raccoon travel corridors were likely more vulnerable. Second, if raccoons began foraging from one of the non-marsh habitat areas adjacent to or within the study area, their general home range size and daily movement capabilities easily encompassed many clapper rail nests (unpublished data). Third, I used HH water levels in my nest survival analyses and detected large differences in survival when water was still present (i.e., at least 1.62 m) (Figure 4.5). At low tide, most of the marsh, including where rails nested, was not covered in standing water, or the standing water was low (< 41 cm) (personal observation), further facilitating raccoon travel. In particular, many tidal creeks were reduced to completely exposed mud. Though raccoons may not be limited by travel distances in the tidal marsh per se, rising tides will limit foraging time and essentially distance by flooding travel corridors. Major waterways were not drained dry at low tide; however, I observed a swimming raccoon and a raccoon in a marsh area accessible only via swimming, even at low tide, suggesting that the main river and creeks were impediments but not impenetrable barriers. Fourth, the freshwater marsh studies referenced above found a positive relationship between nest survival and water depth with no decline in survival past a depth threshold, contrary to what I observed in this study. But, no flood events occurred during those study periods in natural marshes and in other areas the water levels were controlled by land managers. Thus, water levels may never have crossed the threshold beyond which survival would decrease.

Another potential nest predator affected by water levels is the marsh rice rat. Documentation of rice rat movement patterns is scarce, but rats sought taller vegetation or upland areas during times of flooding (Kruchek 2004), facing similar travel challenges to raccoons but on a smaller scale. This species was found to prefer animal-based foods during summer months in a Georgia study (Sharp 1967). Although Sharp (1967) found no evidence of an avian component in the rats' diets, he characterized depredation of the long-billed marsh wren (*Telmatodytes palustris*) nest as an "incidental food source" based on results from an earlier work. Marsh rice rats would likely depredate rail nests as well. I observed rodent droppings within eggshells at six separate nests.

Avian nest predation was one factor not expressly considered in this study that may shift the relationship between the two predictors and nest survival. I found no conclusive evidence of avian nest predators but they may have visited clapper rail nests. The fish crow (*Corvus ossifragus*) is the most commonly reported avian predator of clapper rail nests, but predation events varied regionally. In Florida and South Carolina, the number of rail nests lost to fish crows was much greater (Fargo 1927, Blandin 1965) than studies in both New Jersey and Virginia reported. The few incidents of fish crow depredation in the two latter states were related to proximity to upland habitats or to places with fewer laughing gull nests, which crows regularly depredated (Mangold 1974, Meanley 1985). I rarely observed fish crows in my study system.

Nevertheless, proximity of rail nests to upland areas may have increased susceptibility to fish crows, or other unidentified avian nest predators, as in the New Jersey and Virginia studies. If so, the composite model of nest survival overestimated the effect of terrestrial predators (as measured by the effective cost-distance metric where greater effective distance equals higher nest survival), with some proportion of failed nests depredated by birds instead. Deeper water would not limit avian predators' access to nest sites, lowering peak survival probabilities shown in Figure 4.5. Because avian nest predation appeared minimal, I assumed an equal probability of clapper rail nest depredation by aerial predators regardless of landscape position and did not include it in the survival models. However, if avian depredation is not minimal, but is of equal probability across the landscape, then neither increasing distance nor deeper water afforded the same protective measures to nests as I have inferred from modeling results. In this case, the slopes of the lines representing the positive relationship between survival probability and distance from non-marsh habitat would be flattened (Figure 4.6). Again, peak survival probabilities would be lowered (Figure 4.5). The degree to which the relationships among these parameters would shift depends on the amount of avian nest predation and whether distance from upland areas affects that predation rate.

The data did not support my prediction that local scale variables, essentially vegetative cover measured as vegetation height and density, would best predict nest survival. Interannual variability reduced the usefulness of these metrics in modeling survival. During June and July 2009, the U.S. East Coast experienced elevated sea levels resulting from a combination of NE/SW wind direction, reduced atmospheric pressure, and weakened transport capability of the Florida Current (Sweet et al. 2009). In late June 2009, elevated sea levels combined with perigean spring tides to exacerbate coastal flooding. High tides in my study area were as much as 0.6 m above the predicted values and water washed onto some of Nemours Plantation's dike roads bordering the study area which was an uncommon occurrence (W. E. Mills, personal communication). High tides of this magnitude did not occur in 2010.

In 2009 only, the local model of nest survival was best supported by the data; in 2010 only, the tide-height model was best supported. For both years, none of the parameters was significant except the tide parameter in the 2010 analysis. Surprisingly, the tide parameter did not appear in any of the top 5 models for 2009, whereas in 2010, a year with typical tidal conditions, tide was the single most informative parameter. But, successful reproduction for clapper rails is not an untested process. Regular water level fluctuation from tidal flows is a unique feature to this system and one to which its residents have necessarily adapted. In a breeding season with normal water level fluctuations, flooding would destroy some proportion of nests and predators would destroy another, with the remainder surviving. Within an average year (e.g., 2010), significant differences in local nest site characteristics between successful and unsuccessful nests (Figure 4.7) may not be definitive enough to outweigh the predictive power of tidal influences because tide both directly and indirectly (via moderating predator mobility) impacts nest survival. In the anomalous summer of 2009, when sea level was uncharacteristically high, the underlying relationship between local scale nest site characteristics of successful nests and water levels was decoupled. Therefore, those nests that survived were best described by local conditions and not water height.

Clapper rails selected nest sites based on the landscape scale parameter, seasonal maximum HH water, choosing sites with lower values than the randomly available sites. This choice, in part, corresponded to increased nest survival (Table 4.10). Lower tidal maxima translated to reduced risk of a flooded nest, but lower tidal maxima also facilitated movement of terrestrial predators. Rails selected nest sites based on two local-scale parameters, amount of bare ground present and stem density, but these variables and the other local variables were poor predictors of nest survival across years (Table 4.9). Less bare ground and greater stem density at a nest site indicated the potential for greater nest concealment. In some cases better nest concealment limits predator detection (Martin 1993). Others have found no connection between increased concealment and reduced depredation (Jobin and Picman 1997) in particular if nest predators were generalists (Howlett and Stutchbury 1996). An important nest predator in this system, the raccoon, may forage opportunistically along tidal creeks and edges of waterways near where clapper rails generally placed nests. Therefore, rails' selections of nest sites with greater concealment were less effective at avoiding nest depredation than the overall position of the nest sites in the marsh. Rails did not select nest sites based on distance to terrestrial predator sources, but this landscape-scale variable was important in predicting nest success across years based on the composite model of nest survival (Table 4.10). Successful nests were effectively 1.27 times farther (but not significantly so: $t = 1.23$, $df = 80$, $p = 0.111$) from non-marsh habitat than depredated nests based on the cost-distance values.

CONCLUSIONS

Results of this study showed that breeding habitat quality for clapper rails was affected by tidal height and proximity to potential predators. In this system rails' nest site selections at a landscape-scale were adapted to tidal fluctuations such that their nests rarely failed from flooding. But these same nest sites did not necessarily limit the threat from terrestrial nest predators because the locations were selected without respect to distance to potential sources of these predators. This mismatch between selection and reproductive outcome could have arisen from the random nature of nest depredation by terrestrial predators, from other overriding factors driving selection at that scale (e.g., food availability, intraspecific competition), or from increased terrestrial predator populations to which rails were not adapted.

Research on several pertinent topics not addressed in this study would improve understanding of what constitutes high quality clapper rail habitat and thus the ability to achieve any relevant management goals. First, uncovering the process by which clapper rails assess tide height across the landscape is necessary because this variable was influential in nest site selection and in prediction of nest survival. Second, determining the effects of intraspecific competition (in general and specifically as it relates to food availability) on rail distribution may explain why rails nested closer to predator sources. Third, a directed investigation of clapper rail nest predators would resolve current ambiguity on the proportion of terrestrial versus aerial predators. Probably the best method to distinguish reliably between avian and terrestrial nest predation and to quantify their respective effects would be a camera study, although the tidal marsh system would introduce numerous challenges to its successful execution. Finally, this work was conducted in one portion of coastal South Carolina's marshes. Replicating these efforts in more locations and across the full range of clapper rail marsh habitats, i.e., purely saline to brackish, will determine if the characteristics of rail breeding habitat discovered here broadly apply.

Although there remains much to discover about clapper rails, this work can provide some assistance to managers in developing conservation plans focused on maintaining stable rail populations. The presence of patches of tidal marsh habitat which maximize distances to non-marsh habitats serving as refugia for raccoons and other terrestrial predators may enhance clapper rail nest survival.

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Table 4.1. Descriptive statistics for predictor variables included in logistic regression models of clapper rail nest daily survival rate (DSR) (n =95).

Predictor	**Mean**	**Standard deviation**	**Minimum**	**Maximum**
Landscape variables				
Observation interval's maximum HH water (m)	2.08	0.17	1.62	2.65
Predator cost-distance to nest	1992.67	1790.67	103.99	5752.30
Local variables				
Distance from nest to vegetation edge (m)	3.61	3.03	0.59	28.80
Mean grass height at nest site (cm)	146.61	36.70	61.75	293.00
S. alterniflora stem density (# stems/0.25 m^2)	31.77	10.09	0	63
Bare ground at nest site (%)	38.46	19.58	0	98

Table 4.2. Biological hypotheses and corresponding conditional logistic regression models describing local scale nest site selection by clapper rails.

Hypothesis	**Model**
Global	distance to edge + mean grass height + stem density + % bare
Tide avoidance: distance to edge (flowing water) and grass height combine to protect nest site from high tide	distance to edge + mean grass height
Predator and tide avoidance: distance to edge, grass height, and % bare protect nest from tide and predators	distance to edge + mean grass height + % bare
Predator avoidance: mean grass height, stem density, and lack of bare ground protect nest site from predators	mean grass height + stem density + % bare
Height: site choice based only on grass height, i.e., tide and predator avoidance	mean grass height
Density: site choice based only on number of stems, i.e., predator avoidance	stem density
Distance: site choice based only on nearness to flowing water, i.e., tide avoidance	distance to edge
% Bare: site choice based only on amount of bare ground, i.e., predator avoidance	% bare

Table 4.3. Table outlining biological hypotheses and corresponding logistic exposure candidate models of clapper rail nest daily survival rate (DSR).

Hypothesis	**Model**
Global with year	intercept + year + Julian date + maximum tide + maximum tide^2 + predator distance + distance to edge + mean grass height + stem density + % bare + all interactions from models below
Global without year	intercept + Julian date + maximum tide + maximum tide2 + predator distance + distance to edge + mean grass height + stem density + % bare + all interactions from models below
Constant survival (null)	intercept
Year: DSR due to year nest active	intercept + year
Local effects: DSR due to factors at the nest site scale	intercept + year + mean grass height + distance to edge + stem density + % bare
Predator-tide : DSR due to factors at landscape scale—source of terrestrial predators (location in marsh) and tide influence	intercept + year + maximum tide + maximum tide^2 + predator distance
Date-location: DSR due to time in breeding season nest is active and location (in marsh and at the site)	intercept + year + Julian date + predator distance + mean grass height
Date-tide interaction: DSR due to time in breeding season nest is active, the maximum tide during an observation interval and the interaction between tide height and day of breeding season nest is active	intercept + year + Julian date + maximum tide + maximum tide^2 + maximum tide*year
Date: DSR due to time in breeding season nest is active	intercept + year + Julian date
Predator-height: DSR due to location in relation to predator source and grass height and interaction	intercept + year + predator distance + mean grass height + predator distance*mean grass height
Predator-density: DSR due to location in relation to predator source and stem density and interaction	intercept + year + predator distance + mean grass height + predator distance*stem density

Table 4.3 cont'd.

Predator-date: DSR due to location in relation to predator source and date in breeding season and interaction	intercept + year + predator distance + Julian date + predator distance*Julian date
Predator-tide-date: DSR influenced by tide height, time in breeding season, and distance to predator source	intercept + year + predator distance + Julian date + maximum tide + maximum tide^2
Density-height: DSR due to number and height of stems at nest site and interaction	intercept+ year + stem density + mean grass height + stem density*mean grass height
% bare-height: DSR due to height and amount of cover at nest site and interaction	intercept + year + % bare + mean grass height + % bare*mean grass height
Tide-height: DSR due to tide height and grass height and interaction	intercept + year + maximum tide + maximum tide^2 + mean grass height + maximum tide*mean grass height
Tide: DSR due to maximum tide experienced by nest	intercept + year + maximum tide + maximum tide^2

Table 4.4. Descriptive data for clapper rail clutches during 2009 and 2010.

Complete Clutch data	**2009**	**2010**
Nests	37	58
Mean # eggs per clutch	7.38	7.64
Standard deviation	2.03	1.82
Range	4 to 11	3 to 12
Total # eggs	273	443
Incomplete Clutch data	**2009**	**2010**
Nests	11	15
Mean # eggs per clutch	2.64	4.00
Standard deviation	1.75	2.33
Range	1 to 6	1 to 8
Total # eggs	29	60

Table 4.5. Descriptive data for clapper rail chick production in 2009 and 2010.

Chick production	**2009**	**2010**
Nests	18	30
Mean # chicks hatched per clutch	6.06	6.34
Standard deviation	1.51	2.36
Range	4 to 9	1 to 12
Total # chicks	109	191

Table 4.6. Results of landscape scale comparisons (means and standard errors) of seasonal maximum tide between nest sites and landscape sites.

	Seasonal Maximum Tide Height (m)	
	Nest site	**Randomly available site**
2009 pre-breeding	2.380 ± 0.018	2.502 ± 0.023
2009 breeding	2.588 ± 0.020	2.725 ± 0.025
2010 pre-breeding	2.597 ± 0.004	2.682 ± 0.024
2010 breeding	2.371 ± 0.003	2.466 ± 0.018

Table 4.7. Comparison of local nest site selection candidate models using second order Akaike's Information Criterion (AIC_c) and Akaike weights (w_i), where -2* log L is the log Likelihood, and K is the number of parameters.

Model	**-2*log L**	**K**	**AIC_c**	**Δ AIC_c**	**w_i**
Predator avoidance	61.189	3	67.189	0.000	0.644
Global	61.167	4	69.167	1.978	0.230
Predator-tide avoidance	65.349	3	71.349	4.160	0.080
Bare	70.560	1	72.560	5.371	0.046
Height	94.150	1	96.150	28.961	0
Tide avoidance	93.456	2	97.456	30.267	0
Density	127.410	1	129.410	62.221	0
Distance	135.250	1	137.250	70.061	0

Table 4.8. Model-averaged parameter estimates, odds-ratios, lower and upper 95% confidence limits (LCL, UCL), and importance weights for the composite conditional logistic regression model of local scale nest site selection by clapper rails. Estimated odds-ratios with an asterisk (*) denote a confidence interval not including 1.

Parameter	**Estimate (standard error)**	**Odds-ratio unit change**	**Estimated odds-ratio**	**Odds-ratio 95% LCL**	**Odds-ratio 95% UCL**	**Importance weight**
Bare ground (%)	-0.067 (0.010)	10	0.514*	0.420	0.628	1.000
Mean grass height (cm)	0.019 (0.054)	20	1.472	0.180	12.041	0.954
Distance to edge (m)	0.014 (0.022)	1	1.014	0.972	1.058	0.310
Density (# stems/0.25 m^2)	0.053 (0.027)	10	1.706*	1.011	2.876	0.873

Table 4.9. Comparison of daily nest survival candidate models using second order Akaike's Information Criterion (AIC_c) and Akaike weights (w_i), where log L is the log Likelihood, K is the number of parameters, and n-eff is the effective sample size used to calculate AIC_c.

Model	**log L**	**K**	**n-eff**	**AIC_c**	**Δ AIC_c**	**w_i**
Predator-tide	-160.372	5	1144	330.797	0	0.644
Predator-tide-date	-160.187	6	1144	332.447	1.65	0.282
Tide	-163.917	4	1144	335.869	5.071	0.051
Tide-height	-163.318	6	1144	338.711	7.913	0.012
Date-tide interaction	-163.763	6	1144	339.601	8.803	0.008
Global year	-153.599	17	1144	341.741	10.944	0.003
Global no year	-156.055	17	1144	346.653	15.855	0
Predator-date	-168.994	5	1144	348.040	17.243	0
Date-location	-170.660	5	1144	351.373	20.576	0
Predator-height	-170.924	5	1144	351.900	21.103	0
Predator-density	-171.000	5	1144	352.053	21.256	0
Constant (Null)	-175.376	1	1144	352.755	21.958	0
Year	-174.515	2	1144	353.040	22.243	0
Density-height	-172.059	5	1144	354.171	23.373	0
Date	-174.317	3	1144	354.655	23.858	0
Bare-height	-173.691	5	1144	357.434	26.637	0
Local	-173.246	6	1144	358.567	27.769	0

Table 4.10. Model-averaged parameter estimates, odds-ratios, lower and upper 95% confidence limits (LCL, UCL), and importance weights for the composite logistic exposure model of daily nest survival. Estimated odds-ratios with an asterisk (*) denote a confidence interval not including 1.

Parameter	Estimate (standard error)	Odds-ratio unit change	Estimated odds-ratio	Odds-ratio 95% LCL	Odds-ratio 95% UCL	Importance weight
Intercept	-37.634 (11.568)					
Predator cost-distance	0.0002 (0.0001)	500	1.105*	1.002	1.259	0.929
Julian date	0.0007 (0.003)	--	1.001	0.995	1.007	0.293
Maximum HH water^2	-8.180 (2.739)	0.25	0.129*	0.033	0.509	1.000
Maximum HH water	36.587 (11.265)	0.5	8.808E+07*	1128.399	6.874E+12	1.000
Year (2009 v. 2010)	-0.468 (0.309)	--	0.626	0.338	1.162	1.000

Table 4.11. Means and standard errors for parameters measured at clapper rail nest sites (n = 98) and at paired sites (n = 98) (2009 and 2010 data combined).

	Distance to edge (m)	Mean vegetation height (cm)	Bare ground (%)	# stems/0.25 m^2
Nest sites	3.72 ± 0.38	145.82 ± 4.07	38.08 ± 2.08	30.64 ± 1.12
Paired sites	7.21 ± 0.88	113.19 ± 3.75	63.30 ± 1.82	26.75 ± 1.30

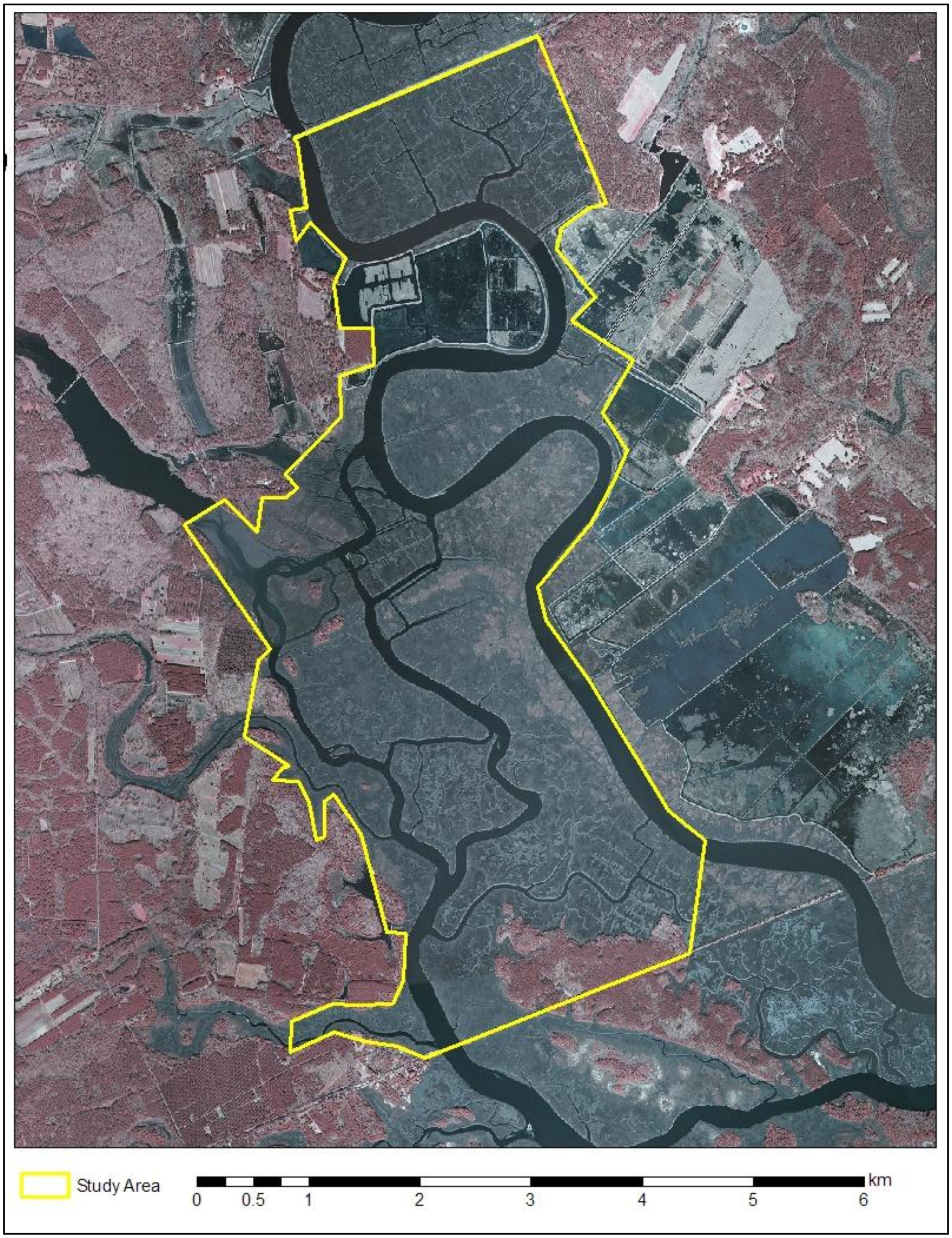

Figure 4.1. Clapper rail nest survival/site selection study area boundary: at the northern end, the U.S. 17 bridge crosses the Combahee River, the western edge abuts mainly Nemours Plantation Wildlife Foundation, the eastern edge is adjacent to other privately owned plantation property, the southern edge is the Wimbee Creek boat landing.

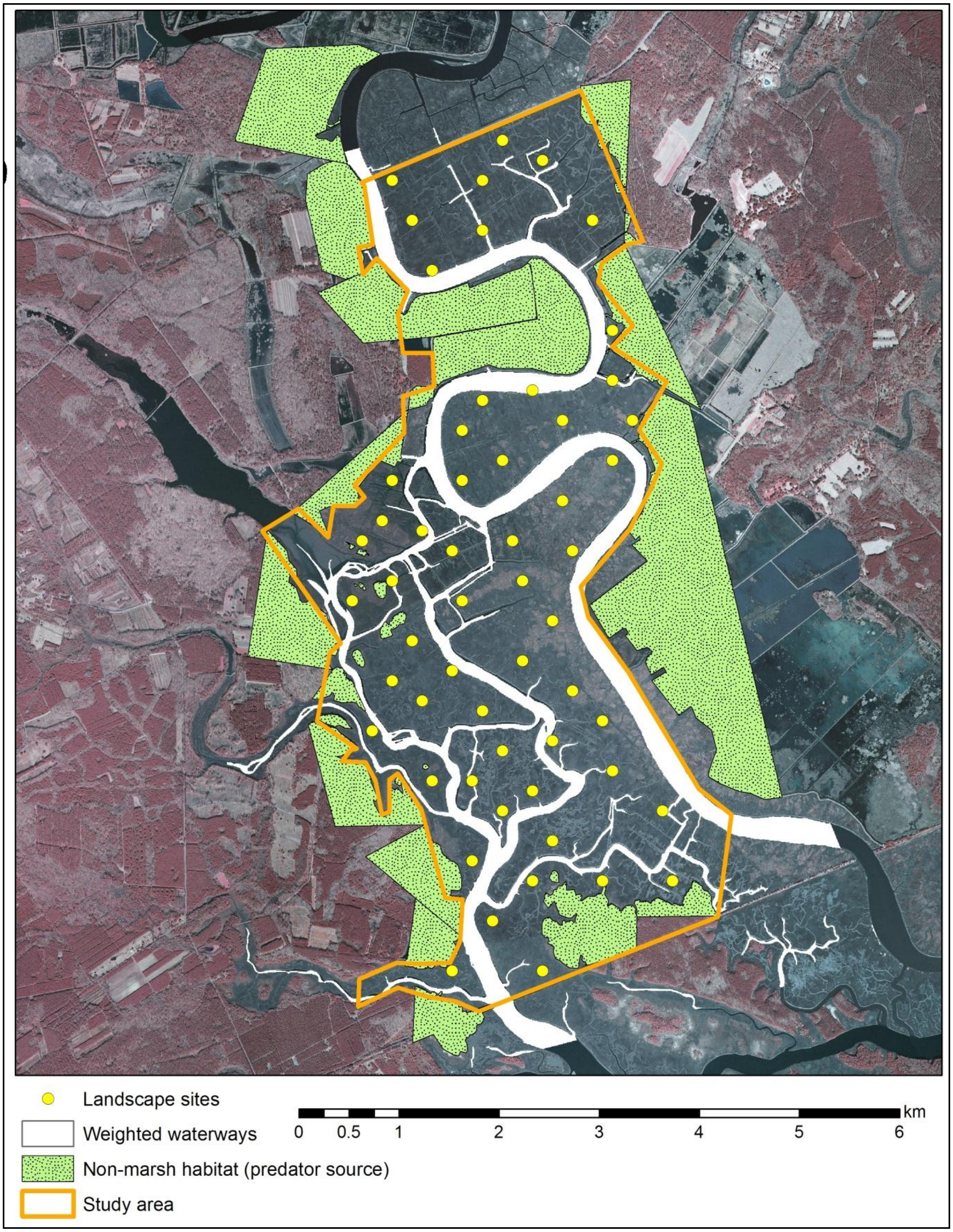

Figure 4.2. Digitized non-marsh habitat (terrestrial predator sources) and weighted main river channels are both layers in the cost-distance surface created to estimate the effective distance a predator would travel to reach each nest site or randomly available (landscape) site.

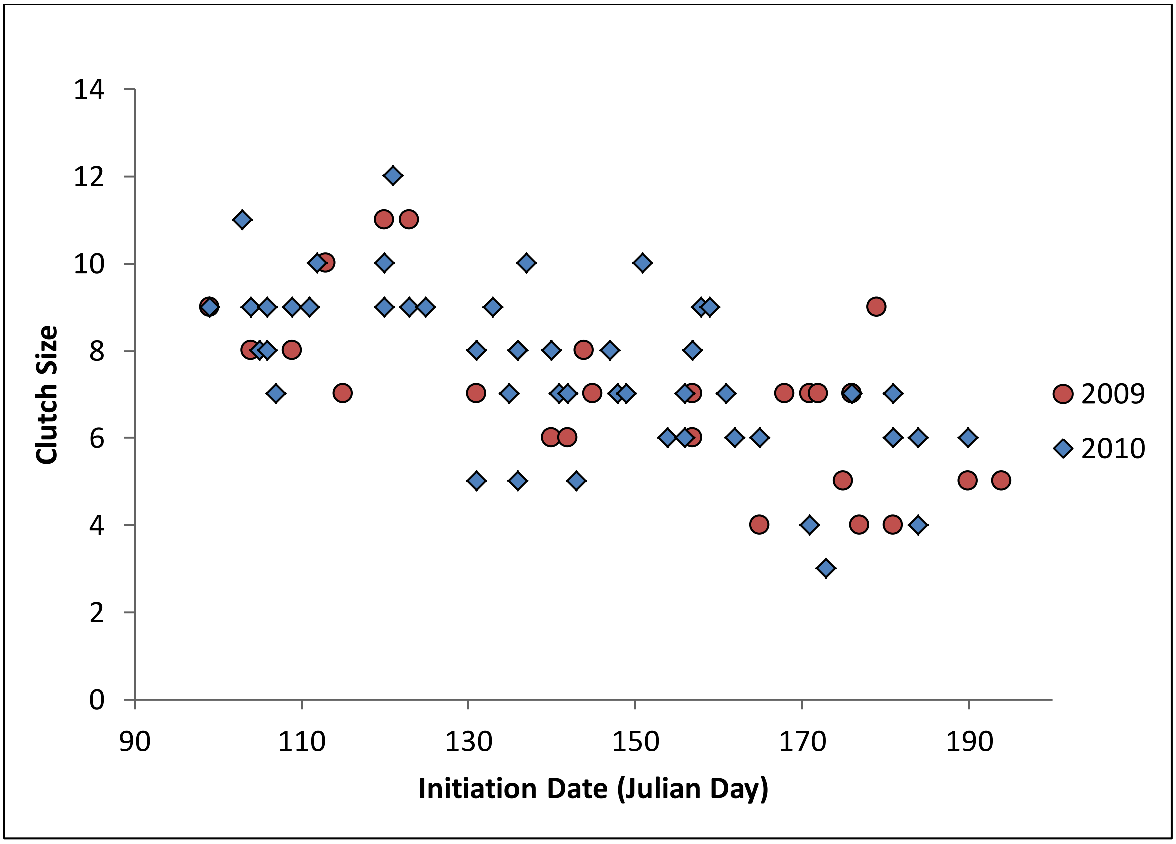

Figure 4.3. Clapper rail clutch size decreased within each breeding season.

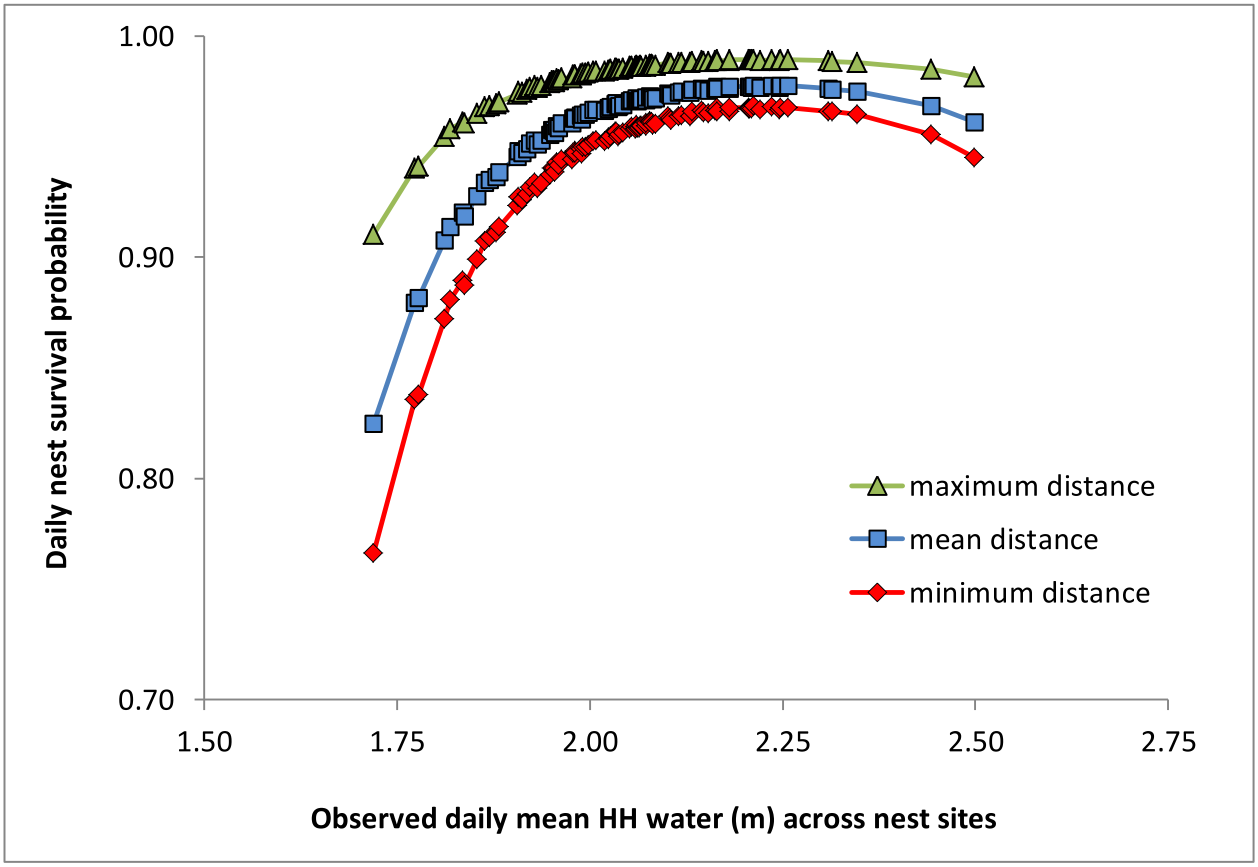

Figure 4.4. Clapper rail daily nest survival probabilities across the range of daily mean HH water (m) observed at active nest sites. Lower HH water values, and very high HH water values, corresponded to lower survival probability. Minimum cost-distances to non-marsh habitat (i.e., sources of terrestrial predators) also corresponded to lower survival probability regardless of HH water value. (Note the truncated values on each axis).

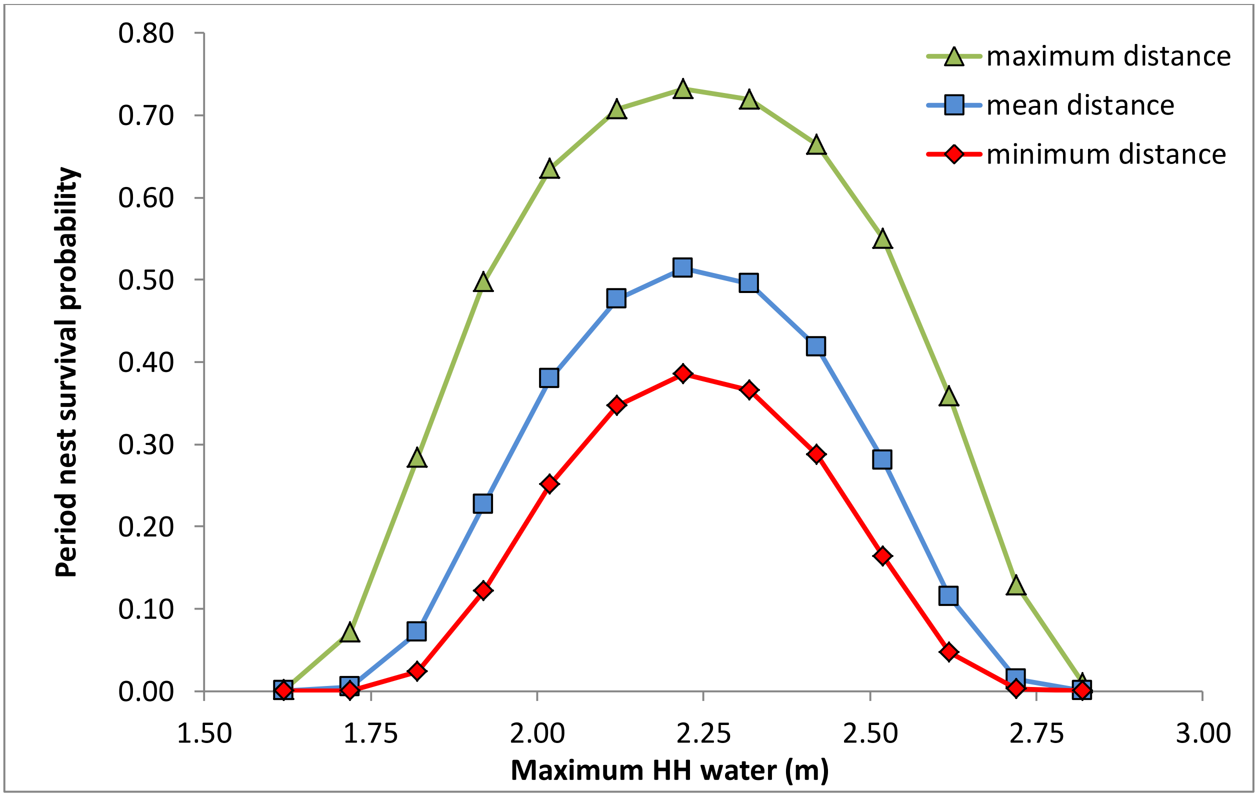

Figure 4.5. Clapper rail nests' period survival probabilities across a range of maximum HH water values at three different distances to non-marsh habitat: the mean, maximum and minimum values calculated. Period survival peaked at an intermediate HH water height of approximately 2.2 m. Lowest survival probabilities corresponded to both extremely low and extremely high HH water levels, regardless of distance.

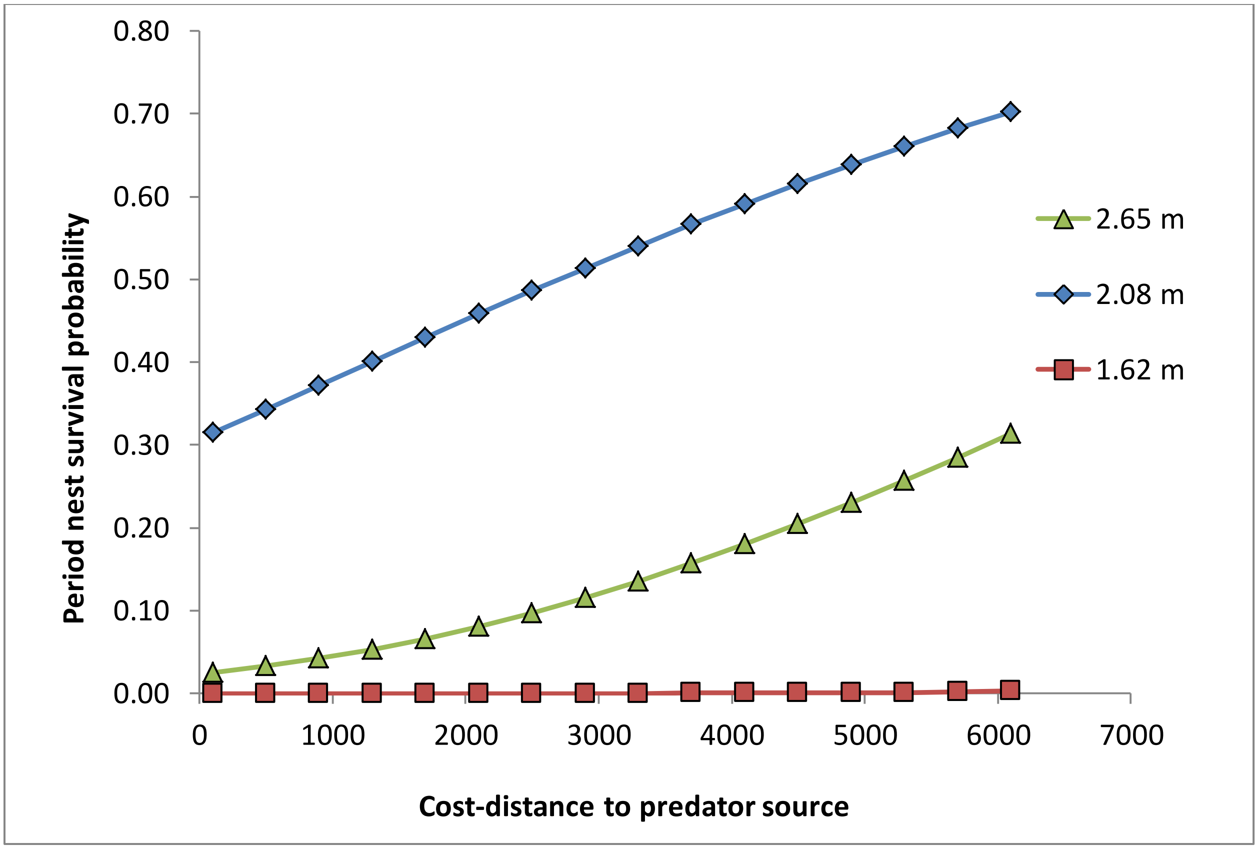

Figure 4.6. Clapper rail nests' period survival probabilities across the range of cost-distance values to sources of terrestrial predators (i.e., non-marsh habitat) at three different HH water heights: the mean, maximum and minimum values observed. Period survival was most likely when water was at a mean height (2.08 m), regardless of distance. Survival increased as cost-distance increased for nests at mean and maximum HH water values.

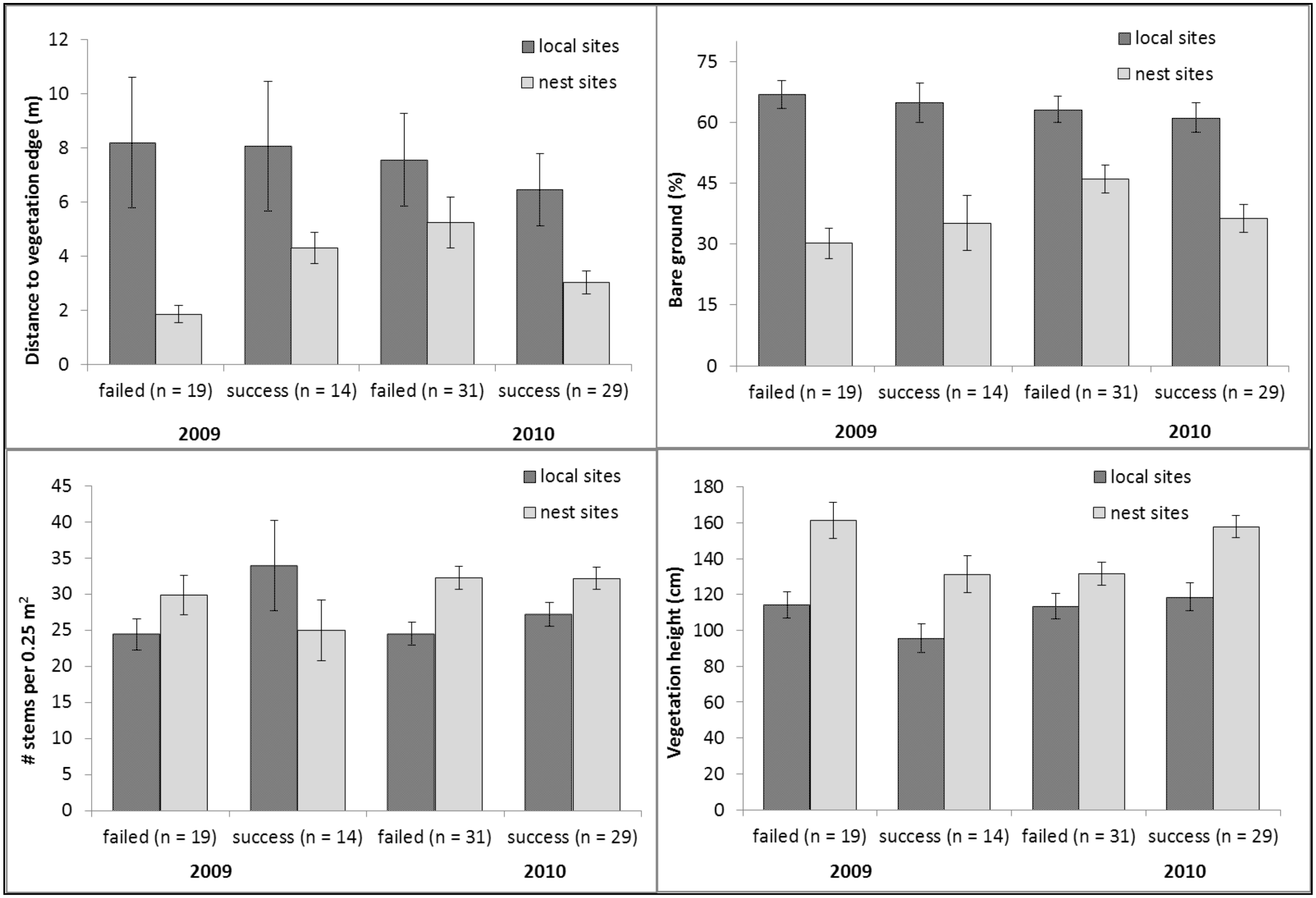

Figure 4.7. Successful nest sites in 2009 were farther from an edge, had shorter vegetation, and lower stem density compared to successful nest sites in 2010. In 2009, failed nest sites were twice as close to an edge and had taller vegetation than successful sites. In 2010, failed nest sites were 1.7 times farther from an edge, had shorter vegetation, and a higher percentage of bare ground present than successful sites. For comparison, characteristics of the local sites paired with each nest site and standard error bars are shown.

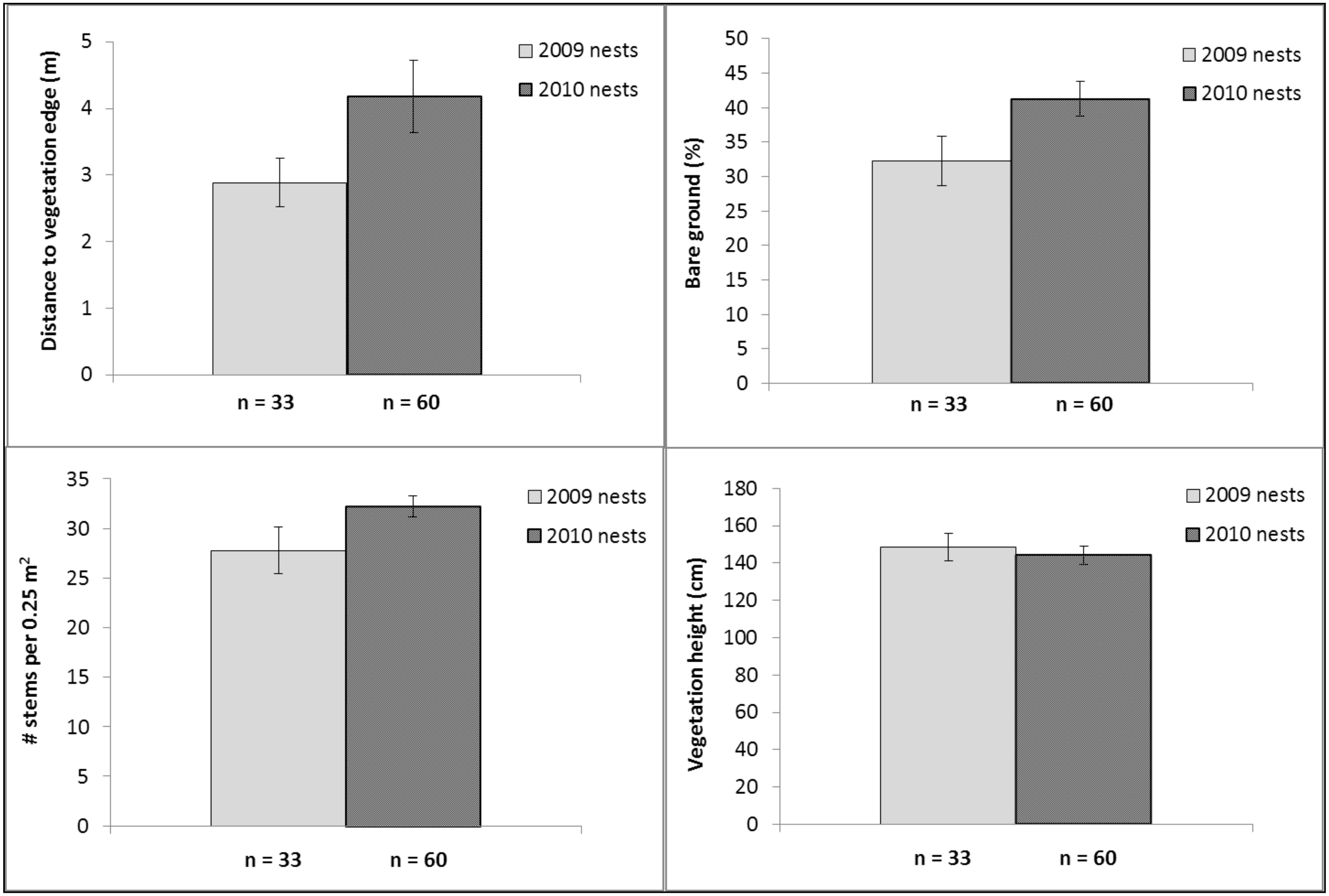

Figure 4.8. Clapper rail nests averaged 1.29 m farther from an edge in 2010 versus 2009. Nest sites in 2010 had slightly higher stem density and percentages of bare ground present than 2009 nest sites. Mean vegetation height at all nest sites was essentially the same for both years. Standard error bars are shown.

CHAPTER 5

SUMMARY

The overall goal of this project was to understand how rails select habitat, what comprises their selected habitats, and how these choices affect survival and reproductive success. Initially, I planned a comparative approach between the mainly freshwater to brackish wetland dwelling king rail and the brackish to saline tidal marsh dwelling clapper rail. Previous work comparing life history characteristics of resident coastal tidal marsh sparrows to their close relatives of non-tidal marsh habitats has illustrated the adaptations used by coastal species (Greenberg et al. 2006). I hoped to investigate whether members of another family of birds (i.e., Rallidae) have adapted their life history to tidal marsh systems in ways similar to sparrows. Unfortunately, my inability to catch an adequate sample of king rails prevented this analysis (see Appendix A for a king rail summary). Nevertheless, from my research I was able to explore how clapper rails address the inherent tradeoffs facing residents of coastal tidal marshes.

From a management perspective, I continued an effort to assess the capacity for the thousands of hectares of coastal wetland impoundments in South Carolina to function as supplemental rail habitat. Additionally, I contributed to the information needed on rails as described by the Association of Fish and Wildlife Agencies' Migratory Shore and Upland Game Bird Support Task Force (MSUGBSTF 2009). I provided the first estimates of demographic parameters for Atlantic Coast clapper rails which will facilitate the estimation of population trends. I also described the connection between these demographic parameters and specific habitat characteristics. No previous study of Atlantic Coast clapper rails has investigated these relationships. This information can assist in harvest and land management decision-making for these gamebirds.

In Chapter 2, I described the effort to determine the sex of each captured rail. Genetic testing of blood and feather tissues was used to identify the sex of 82 clapper rails. I also explored the likelihood of using morphometric measurements to determine sex in the field. My results were similar to those of a study conducted in Louisiana (Perkins et al. 2009), suggesting that a region-wide morphometric model would likely be based on wing, culmen, and possibly tarsus measurements. Knowing the sex of study individuals enhances population modeling efforts. A limitation that still exists for king and clapper rails is a definitive indicator of age (Pyle 1997). The age-structure of a population is also important when evaluating demographic rates and population trends. To date, no large-scale effort has focused on aging king or clapper rails.

In Chapter 3, I evaluated habitat selection for clapper rails by comparing habitat characteristics at the local and landscape scales between observed and simulated home range sites. I found that during the breeding season, male and female clapper rails occupy home ranges of similar sizes and habitat characteristics. Because both sexes incubate an active nest and tend to young broods (Meanley 1985) this result was consistent with expectation. Clapper rails' home range selection is likely driven by food availability as observed home ranges had greater amounts of foraging area than simulated home range sites. Observed home ranges also contained greater amounts of bare ground at sampling locations which may serve as a proxy indicator for food availability in the interior of clapper rail home ranges. The results of this research suggest the next step would be to conduct an explicit study of the distributions and densities of prey items within a clapper rail's home range (e.g., Rush et al. 2010a) compared to what is available across the landscape.

I modeled adult survival of radio-marked birds which is the first assessment of this demographic parameter for Atlantic Coast clapper rails. Survival was higher in 2010 compared to 2009. A majority of deaths during the study period occurred in late winter and early spring, especially in 2009. The timing of the mortality events suggests that survival of these animals may differ across seasons and a year-round telemetry study would aid in resolving this question. Clapper rails may have a higher survival probability with increased foraging area in a home range, but survival may be lower with increased amounts of bare ground present. Males may have a higher survival probability than females. Expanding the sample size of radio-marked rails and conducting specific experiments related to these covariates would clarify their relationships to adult rail survival.

In Chapter 4, I evaluated clapper rail nest site selection at the local and landscape scales and related these choices to reproductive success, specifically nest survival. Clapper rails chose nest sites with lower tidal maxima than available sites. This selection contributed, in part, to increased nest survival; however, lower tidal maxima also facilitated the movement of terrestrial nest predators. Local-scale habitat characteristics selected by rails indicated that nest sites had better concealment than locally available alternative sites but these characteristics were poor predictors of nest success. Nest concealment may not reduce depredation by generalist predators such as the raccoon. Most nests in this system failed due to depredation, not tidal flooding as was strongly implicated in reports from New Jersey (Kozicky and Schmidt 1949, Mangold 1974). Nest depredation was cited by multiple southern studies as a main factor rather than flooding (Fargo 1927, Adams and Quay 1958, Blandin 1965, Meanley 1985). Nests were more likely to fail the closer their proximity to non-marsh habitat, presumably a source of terrestrial predators like the raccoon. A study focused specifically on the nest predator assemblage would clarify the main threats to rail nests. It would be beneficial to revisit the study areas of the earlier works, given that all are more than 25 years old, to detail current reproductive activity of clapper rails and any changes in causes of nest failure. Beyond a strict assessment of nest success, a study focused specifically on post-hatch survival would permit an estimation of recruitment which is a key factor in understanding population dynamics.

In coastal tidal marsh systems it is often difficult to ascertain characteristics of high quality habitat for a number of secretive resident avian species, including rails, because of human inaccessibility to habitat and low detection rates with high variability (Gibbs and Melvin 1993, Conway and Gibbs 2005). However, in this thesis I have shown that by using radio-telemetry, valuable data can be gathered on these animals. There are few studies available with which to directly compare my results for clapper rail survival and reproductive success, and none for Atlantic Coast rails. This fact makes a determination of habitat quality somewhat arbitrary, especially because my study does not capture long-term data. Adult survival was variable across years but similar between sexes in each year; breeding season survival was high. My estimate of rail daily nest survival was < 0.02 lower than a Mississippi study (Rush et al. 2010b). A mean of 6.2 chicks were produced from successful nests across years. Unless recruitment and adult survival in the non-breeding season are low, this study area represents high quality clapper rail habitat and could be used as a model system for land managers.

This project originated from an interest in supplementing king and clapper rail habitat by managing the thousands of hectares of coastal wetland impoundments in South Carolina in ways beneficial to these species. King rails in this study area are known to use impoundments of the ACE Basin National Wildlife Refuge, but I was unable to capture enough king rails to determine what specific features of the impoundments contributed to the rails' habitat choices . In North

Carolina and Virginia, king rails used impoundments but occupancy was lower than in non-impounded wetlands and prescribed fire regimes encouraged a positive response in king rail occupancy in both areas (Rogers 2011). Clapper rails were never detected in the managed impoundments at Nemours Plantation, but were observed on levies and the fringe marsh between the impoundments and the Combahee River.

Now that we have baseline information on specific habitat requirements, experimental manipulation of the vegetation and water levels within an impoundment could be implemented to determine if clapper rails would use this managed habitat. A major part of the manipulation to water levels would consist of mimicking the tidal fluctuations of natural marsh areas such that fiddler crabs could populate the impoundment.

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APPENDIX A: KING RAIL (*RALLUS ELEGANS*) SUMMARY

Appendix A contains a summary of the data collected on king rails during this study.

The airboat method of capturing clapper rails (Chapter 3) was unsuccessful in catching king rails in this study. I focused airboat capture efforts in known king rail habitat upriver from the clapper rail study area in both the open water marshes of the Combahee River and the impoundments of the ACE Basin National Wildlife Refuge. However, a combination of low water levels (even on spring tide nights in the river) and tall, dense vegetation prevented detection and capture of king rails. King rail populations also appeared to be lower than clapper rail populations in this area (personal observation).

I used alternative methods to catch four king rails at the Combahee Fields Unit of the ACE Basin National Wildlife Refuge in Colleton County, South Carolina. In 2009, I captured three king rails; two via a drop-door trap, and one using a dip net. In 2010, I captured one king rail in a drop-door trap. I submitted tissues for genetic sexing of the 2009 birds only (see Chapter 2 for methods). I measured all birds and attached radio-transmitters following the description in Chapter 3 (Table A.1). One male from 2009 (USFWS band #1065-33145) died within two weeks of capture. I was not able to retrieve this transmitter or the bird’s carcass.

I tracked king rails by driving or walking the levies along the impoundments within Combahee Fields. In 2009, I began following the two rails after their capture on April 16. I tracked the male until June 9 when I no longer detected a signal (41 locations acquired). I tracked the female until July 30, after which I stopped radio-telemetry for that year (61 locations acquired). In 2010, I followed the king rail (sex unknown) from capture on June 21 until August 4 which was the end point of the radio-telemetry study (29 locations acquired).

I calculated home ranges for three king rails following the methodology in Chapter 3 (Figure A.1). The home range size for the female was 9.93 ha; the male home range was 0.69 ha; and the rail of unknown sex home range was 7.05 ha. I sampled habitat metrics at 10 points within the home ranges for the 2009 king rails. The mean vegetation height for the female was 162.23 cm, and for the male, 126.22 cm. The mean distance to water's edge was 17.45 m for the female and 6.49 m for the male. I summarize the plant species found within each bird's home range in Table A.2.

I found a single king rail nest on June 24, 2010 which belonged to the bird with the radio-transmitter (Figure A.1). This nest had seven eggs present upon discovery. On July 9, I observed one egg with a hole and a chick active inside the egg. On July 12, the nest was empty and the radio-marked bird had moved 900 m southwest to the marsh fringing the Combahee River where it remained for the rest of the study period (i.e., until August 4, 2010).

Table A.1: Morphometric measurements of four king rails captured in 2009 and 2010 plus the genetically identified sex of the three 2009 birds.

USFWS Band	Sex	Body Mass (g)	Unflattened Wing Chord (mm)	Exposed Culmen (mm)	Tail Length (mm)	Tarsus Length (mm)	Middle Toe Length (mm)
1065-33145	M	226	162	55	63	62	45
1065-33146	F	327	159	58	54	52	43
1065-33147	M	373	166	64	54	62	56
1065-33195	unknown	373	172	65.3	65	66.9	54.4

Table A.2: Plant species found within two king rail home ranges at the Combahee Fields Unit of the ACE Basin National Wildlife Refuge in 2009.

Plant species	2009 male home range	2009 female home range
Spartina cynosuroides		x
Schoenoplectus robustus	x	x
Typha spp.	x	x
Sesbania spp.	x	x
Setaria magna	x	x
Schoenoplectus tabernaemontani	x	x
Zizaniopsis miliacea		x
Erechtites hieraciifolia	x	
Cyperus spp.	x	
Echinochloa crus-galli	x	
Polygonum spp.	x	
Panicum spp.	x	
Pluchea spp.	x	

Figure A.1: Adaptive-LoCoH 90% home ranges for three king rails and one nest location within the Combahee Fields Unit of the ACE Basin National Wildlife Refuge in Colleton County, South Carolina.

APPENDIX B: CLAPPER RAIL (*RALLUS LONGIROSTRIS*) MORPHOMETRIC MEASUREMENTS

Appendix B contains a table of the morphometric measurements collected for clapper rails captured in 2009 and 2010.

Table B.1. Morphometric measurements and genetically identified sex of clapper rails captured during 2009 and 2010.

USFWS Band	Sex	Body Mass	Unflattened Wing Chord	Exposed Culmen	Tail Length	Tarsus Length	Middle Toe Length
1065-33108	M	275	153	66.76	69	48.61	36.84
1065-33109	M	270	159	66	65	57	42
1065-33110	M	275	152	65	66	57	42.5
1065-33111	M	250	148	65.75	53	55	43.5
1065-33112	F	215	140	59	55	52	41
1065-33113	M	270	156	67.5	70	56	45
1065-33114	F	200	140	61	60	49	40
1065-33115	F	175	144	63.5	65	53	38.5
1065-33116	M	250	146	65	62	51	38
1065-33117	M	230	159	68	66	51.5	43.5
1065-33118	M	240	149	66	62	52.5	43
1065-33119	M	228	156	63	63	54.5	41.5
1065-33120	M	215	143	61.5	56	55	37
1065-33121	M	250	135	59.5	60	48	40
1065-33122	M	232	160	62	65	48.5	44
1065-33123	M	205	147	58.5	61	44	37
1065-33124	F	220	143	60	49	49	40
1065-33125	F	200	135	59	61	46	40
1065-33126	M	230	147	65	63	54	39
1065-33127	F	195	141	56.5	63	50	40.5
1065-33128	M	233	150	70	66	54	42
1065-33129	F	225	139	61	61	47	40.5
1065-33130	M	210	145	59	62	50	38
1065-33131	M	240	152	65.5	66	53.5	43
1065-33132	M	295	156	67	72	56	43
1065-33133	F	215	135	59	55	49	34
1065-33134	M	295	144	65	55	51	36
1065-33135	M	240	150	61	79	54	46
1065-33136	M	280	145	65	60	58	49
1065-33137	M	270	148	60	60	59	46
1065-33138	M	225	138	63	67	52	44
1065-33139	F	240	138	61	55	49	36
1065-33140	M	295	143	70	59	54	40
1065-33141	M	280	146	66	60	48	39
1065-33142	M	255	145	60	57	51	39
1065-33143	F	205	144	64	68	48	46
1065-33144	M	280	152	70	58	49	40
1065-33148	F	320	140	55	57	53	42
1065-33149	F	280	137	56	55	51	40
1065-33150	F	310	128	56	57	48	36
1065-33151	M	267	149	68	56	57	42
1065-33152	F	239	139	57	57	52.4	46.2

Table B.1 cont'd.

USFWS Band	Sex	Body Mass	Unflattened Wing Chord	Exposed Culmen	Tail Length	Tarsus Length	Middle Toe Length
1065-33153	M	225	147	64	56	55	38
1065-33155	F	233	136	63.4	61	51.4	40.7
1065-33156	M	283	144	63	57	54.4	45.4
1065-33157	M	343	157	63.2	62	57.2	40.3
1065-33158	F	237	151	57.8	60	51.9	44.6
1065-33159	M	303	152	65.6	61	50.9	46.2
1065-33160	F	206	132	57.5	59	44.8	42
1065-33161	M	312	150	62.5	61	50.3	46.2
1065-33162	M	268	145	57.5	60	43.8	45.2
1065-33163	F	245	139	58	55	50.5	45.5
1065-33164	M	298	150	66.8	59	48.3	47.2
1065-33165	M	344	156	67.3	58	51.8	50.8
1065-33167	F	232	143	55	53	47.7	42.3
1065-33168	M	313	152	64.7	59	53.8	50.6
1065-33169	M	284	154	65.4	64	54.5	50.3
1065-33170	F	212	136	62.2	54	46.7	38.8
1065-33171	F	214	135	59	56	47.6	44.9
1065-33172	M	288	150	67.4	62	56.8	49
1065-33173	F	323	148	61.8	56	55.1	47.2
1065-33174	M	253	137	56.7	52	51.7	47.5
1065-33175	M	310	148	71.3	57	55.2	51.7
1065-33176	M	343	152	67.3	61	60.1	55.6
1065-33177	M	312	156	65.7	62	57.6	52
1065-33178	M	308	149	64	59	56.4	51.8
1065-33179	M	300	155	66.2	61	55.2	54.6
1065-33180	M	311	148	68.2	52	53.2	45.4
1065-33181	M	305	151	64	63	54.1	49.2
1065-33182	M	254	144	57.6	52	51.3	46.7
1065-33183	F	212	130	52.3	51	49.5	45
1065-33184	M	298	150	65.1	67	59.4	51.3
1065-33185	F	265	137	60.9	62	50	47.3
1065-33186	M	315	149	60.4	56	57.8	54.4
1065-33187	M	283	149	67.3	60	56.5	53
1065-33188	F	313	148	59.1	55	51.4	41.1
1065-33189	F	243	141	60	52	46.1	41.2
1065-33190	M	300	153	66.5	55	51.8	44
1065-33191	M	308	153	65.3	56	54.2	51.5
1065-33192	F	213	139	61.5	56	48.1	42.7
1065-33193	F	290	140	63.2	61	51.3	46.2
1065-33194	M	312	145	72.4	61	56.3	49.1

APPENDIX C: CLAPPER RAIL (*RALLUS LONGIROSTRIS*) NECROPSY REPORT

Appendix C consists of a necropsy report completed by the staff at the Southeastern Cooperative Wildlife Disease Study in Athens, Georgia, for a male clapper rail found dead in 2010.

DIAGNOSTIC SERVICES SECTION **FINAL REPORT**

SOUTHEASTERN COOPERATIVE WILDLIFE DISEASE STUDY (SCWDS)		**CASE NUMBER**	CC104-10
COLLEGE OF VETERINARY MEDICINE		**DATE RECEIVED**	**April 16, 2010**
THE UNIVERSITY OF GEORGIA		**DATE OF REPORT**	
ATHENS, GEORGIA 30602-7393			
TELEPHONE: 706-542-1741; FAX: 706-542-5865			

STATE SC **COUNTY** Not provided **AREA**

SPECIES (NO.) Clapper rail (1) **SEX** M **AGE** Adult **WEIGHT**

CASE HISTORY: The carcass of an adult, male clapper rail was submitted to SCWDS by Ms. Cathy Ricketts of Warnell School of Forestry and Natural Resources (WSFNR) at the University of Georgia. A backpack transmitter was placed on this clapper rail on April 11, 2010 as part of a WSFNR graduate research project. The bird was found dead two days later. The carcass was collected and frozen until it was submitted to SCWDS for diagnostic examination on April 17, 2010. A necropsy was performed on April 19, 2010 after allowing the carcass to thaw.

FINAL DIAGNOSIS: Undetermined

COMMENTS: The cause of death was not identified in this clapper rail. The necrosis observed in the liver could potentially be a result of blunt trauma, but this could not be confirmed during our examination. The extent of the liver injury was not severe and it most likely did not directly result in the death of this clapper rail.

WILDLIFE IMPLICATIONS: Unknown

PUBLIC HEALTH IMPLICATIONS: Unknown

LIVESTOCK IMPLICATIONS: Unknown

DIAGNOSTICIAN	**SUPERVISOR**
Justin D. Brown, DVM, PhD	Kevin Keel, DVM, PhD, DACVP

DISTRIBUTION: SCWDS File **Laboratory Results Begin on Page 2**

CASE NUMBER CC104-10

GROSS FINDINGS: The examined adult, male clapper rail is in moderate nutritional condition. A silver band is present on the left leg (ID# 1065-33172) and a blank, blue band is present on the right leg. The proventriculus and ventriculus are empty and the intestines contain a small amount of mucoid, tan digesta. No other gross lesions are apparent.

MICROSCOPIC FINDINGS (W10-240):

All of the examined tissues are moderately autolyzed.

Liver: Multiple delineated areas of necrosis are present in the hepatic parenchyma in one examined region of the liver.

Brain, kidney, lung, skeletal muscle, heart, testis, spleen, heart, and gastrointestinal tract: No significant lesions were identified in the organs or tissues listed.

MORPHOLOGIC DIAGNOSIS:

Liver: Moderate, acute, focal, coagulative necrosis of the hepatic parenchyma.

VIROLOGY:

No virus was isolated from a sample of brain submitted to the SCWDS Virology Laboratory for isolation.