MODELING PRODUCTIVITY FOR AMERICAN OYSTERCATCHERS (*HAEMATOPUS PALLIATUS*) AND WILSON'S PLOVERS (*CHARADRIUS WILSONIA*) IN A HIGHLY DYNAMIC ENVIRONMENT

by

ABBY VAUGHAN STERLING

(Under the Direction of Robert J. Cooper)

ABSTRACT

Nest site selection is an important component of breeding ecology for all birds, but beach-nesting shorebirds, which use a restricted and specific habitat, face multiple, significant challenges. I examined how habitat features and nest-site selection influenced several aspects of overall productivity for American Oystercatchers (*Haematopus palliatus*) and Wilson's Plovers (*Charadrius wilsonia*), two species of conservation concern that nest on the Georgia coast. First, I used a multi-scale modeling approach to determine habitat features that best predicted nest site selection and daily survival of nests for both species. The results pointed to a potential mismatch between habitat cues used for nest site selection and those that are predictive of daily nest survival, which could indicate that these sites are acting as an ecological trap and have significant conservation implications. Additionally, I found that nest site selection and nest success were not predicted by the same habitat features for both species, and found that models were better at predicting nest success for Wilson's Plovers than for American Oystercatchers. With these results in mind, I used competing risks models to look at how the dual threats of predation and overwash were influenced by habitat features, and how these threats influenced nest survival of Wilson’s Plovers. I found that predation risk was high, but not well predicted by habitat features and while tidal overwash risk was variable by year, it was better predicted by habitat features, such as elevation and community type. Finally, I estimated fledging success for Wilson’s Plover chicks, and investigated how environmental variables influenced survival. The survival estimates for chicks were low compared to other published estimates, and I found that environmental factors could be influencing nest success and chick survival differently. The results from this study suggest that active conservation efforts focused on multi-species management during both the nesting and fledging stages are necessary for protecting these shorebird species to ensure their viability on the Georgia coast.

INDEX WORDS: American oystercatcher, *Haematopus palliatus*, Wilson’s plover, *Charadrius wilsonia*, Nest survival, Nest site selection, Competing risks, Chick survival, Productivity, Management, Shorebirds

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DEDICATION

This dissertation is dedicated to my dad, Ken Sterling. Although he passed away during my final field season, his unyielding support and encouragement helped get me to this point, and I know he’d be proud and excited to be here at the end with me.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Population declines of North American shorebirds have been noted some for some time, but recent analysis of trends have highlighted that these declines may be more severe than previously projected, and that proactive conservation management is warranted (Morrison and Johnston 2001). Regional and flyway-focused plans have emphasized that species in all life-cycle stages, including wintering, migration, and nesting, are at risk from threats such as loss or degradation of habitat, disturbance, and predation (Brown 2001, Brown 2013). In the Southeastern United States, several species of conservation concern require coastal habitat for at least part of the year. Federally endangered piping plovers (*Charadrius melodus*) from the Great Lakes spend the winter predominately in Georgia and South Carolina (Gratto-Trevor et al. 2012), while federally threatened red knots (*Calidris canutus*) migrate through the region during the fall and spring (Burger et al. 2012). During the nesting season, the American oystercatcher (*Haematopus palliatus*) and the Wilson's plover (*Charadrius wilsonia*), which are designated as species of high conservation concern by the U.S. Shorebird Conservation Plan (Brown 2001), include the beaches of the Southeast in their breeding range. Within Georgia, the American oystercatcher is listed as rare while the Wilson's plover is listed as threatened (GADNR 2015). Research focused on the nesting ecology and overall productivity in Georgia is necessary to fill knowledge gaps and guide management to increase the population of these species within the state.

BACKGROUND ON THE AMERICAN OYSTERCATCHER

The American oystercatcher is a large, charismatic shorebird that is closely tied to marine environments with a breeding range that spans along the East Coast from Maine to Florida, along the Gulf Coast into Texas, the east and west coasts of Mexico, parts of southern California, and south into Argentina and Chile (Nol and Humphrey 2012). Population estimates for this species are around 11,000 individuals (Brown 2001), and in Georgia in 2010, it was estimated that there were approximately 115 nesting pairs (Keyes, personal communication). In Georgia, the breeding season for this species occurs from March through July (George 2002), with the earliest recorded eggs being laid in early March (personal observation). Nests are generally shallow scrapes or depressions on open ground, sometimes lined with shell, wrack or pebbles (Nol and Humphrey 2012). Birds may re-nest as many as three times in a given season if the earlier clutches are lost (George 2002, Nol and Humphrey 2012). American oystercatchers exhibit some flexibility with regard to selection of nesting habitat; previous studies have located nests in traditional, open beach, dune and sand-flat habitats (Corbat 1990, George 2002, McGowan et al. 2005, Sabine et al. 2006, Schulte et al. 2010), as well as on dredge spoil islands, marsh islands (Lauro and Burger 1989, McGowan et al. 2005) and on oyster shell rakes (Nol and Humphrey 2012). They have also nested on rooftops in Florida and on rocky outcrop islands in Massachusetts (Jedry, personal communication).

American oystercatchers have varying rates of reproductive success. Their nesting success, defined as at least one egg hatching, ranges from a high of ~45% (McGowan et al. 2005) to a low of 12% in Georgia (George 2002). Upon hatching, precocial chicks and adults move away from the nest to foraging areas, although adults will provision chicks with food until fledging, which usually occurs around 35 days (Schulte et al. 2010). Fledging rates, when chicks are flighted, are generally even lower than nest success rates: from 54-80% in New York (Zarudsky 1985) to only 5% in Georgia (George 2002). In a more recent study at three islands in Georgia (Wassaw, St. Catherines Island, and Little St. Simons Island) fledging success varied from 12-20% (J. Hilburn, unpublished data, 2010/11). The highly variable rates of success reported in the literature indicate that several factors, such as elevation, predation, and environmental elements at the local level, may be influential in determining success (Sabine et al. 2006, Schulte et al. 2010, Nol and Humphrey 2012, Collins et al. 2016).

BACKGROUND ON THE WILSON'S PLOVER

In Georgia, beach-nesting oystercatchers share a similar habitat with more cryptic Wilson's plovers, which exclusively nest in coastal regions extending from Virginia south to Florida, along the Gulf Coast, into Mexico and Southern California, parts of Central America, and into South America (Corbat and Bergstrom 2000). The breeding season varies by region; in Texas egg laying was documented between mid-April to mid-June (Zdravkovic 2013), in Virginia it was primarily in May (Bergstrom 1988), in Georgia it was mid-April through the end of June (Corbat 1990), while in the Caribbean birds begin laying eggs as early as late February and continued through to early June (Brown and Brindock 2011). Once a nesting territory is established by a pair, the male Wilson's plover makes several simple scrapes in the sand, but the nest scrape is chosen by the female and occasionally is lined with shell or other objects (Corbat and Bergstrom 2000). Birds will re-nest if the first clutch is lost and usually only produce one brood per season. Nesting habitat is typically open sandy areas, overwash flats, dune edges, sparsely vegetated saline flats, and even roadways (Tomkins 1944, Bergstrom 1988, Corbat 1990). Population estimates for this species are at about 6,000, but there is low confidence in this number (Brown 2001), and the breeding population in Georgia was around 300 pairs in 2010 (Keyes, personal communication).

Nest success rates are variable, ranging from 58% (Hood 2006) and 25-54% (Bergstrom 1988) in Texas, to around 45% in North Carolina (Ray 2011), 37.1% in the Caribbean (Brown and Brindock 2011), and 11-55% in Georgia (Corbat 1990). Estimates for age of fledging vary for Wilson’s plovers from 29 days in North Carolina (Ray 2011), to up to 35 days in Louisiana (Zdravkovic 2010). In cases where chicks experience limited disturbance and abundant food and cover resources, fledging may be delayed (Zdravkovic 2013). As with American oystercatchers, reproductive success for Wilson’s plovers is variable with the greatest percentage of failures due to predation and flooding, although human disturbance is also a noted problem (Hood 2006, Brown and Brindock 2011).

CONSERVATION ACTION AND RESEARCH

American oystercatchers warrant conservation action specifically due to small population sizes, loss of habitat and direct and indirect threats including disturbance, contamination of food resources, and increases in nest predators (Schulte et al. 2010). The American Oystercatcher Working Group (AMOYWG), created in 2007 and composed of numerous state, federal, university, and private partners, has shown that dedicated, species-specific management can yield positive results (Brown 2013). Recent estimates show that the population declines of American oystercatchers may have stabilized, although productivity estimates for the state of Georgia remain low (Sabine et al. 2006). While trend information is limited for Wilson’s plovers, populations are thought to be declining and northern contractions to this species range have been documented (Zdravkovic 2013). Within the state of Georgia, management actions such as predator control and habitat management have been implemented with the objective of increasing nest success for American oystercatchers; however, it is not until recently that the focus of shorebird management has been expanded to include Wilson’s plovers, despite the two species nesting sympatrically. This research seeks to answer questions about nest site selection, nest success, and habitat use for both species through several different lenses. It also aims to examine how management focused on American oystercatchers influences Wilson’s plover conservation, as well as reduce knowledge gaps that exist for both species.

Several studies have investigated various aspects of shorebird nest site selection, breeding ecology, and reproductive success and point to a non-random distribution of nests, indicating that there may be several adaptive forces exerted on birds as they attempt to determine a suitable nest site (e.g.,Page et al. 1985, Burger 1987, Brown and Brindock 2011, Ray 2011, Gómez-Serrano and López-López 2014). Habitat choice influences reproductive success, and therefore nest-site selection that maximizes an advantage to the individual should be apparent, especially in heterogeneous landscapes (Martin 1995, Misenhelter and Rotenberry 2000, Jones 2001, Robertson and Hutto 2006, Arlt and Part 2007). However, there are numerous complicating factors that can create disconnects between habitat cues and nest success. Mismatches, where habitat features may not be indicative of high quality habitat, can occur because of changes within the landscape (Kokko and Sutherland 2001) or because reproductive trade-offs exist for an individual (Hunter et al. 2016). Variation within the habitat at multiple spatial scales can provide information to birds selecting nest sites, which can also make patterns between site selection and nest success difficult to assess (Misenhelter and Rotenberry 2000). Furthermore, requirements may differ by species, and these differences could be apparent in nest site selection or nest success within a given habitat (Jaenike and Holt 1991, Martin 1998). Therefore, an understanding of how habitat variables can be used to predict nest site selection as well as nest success should incorporate multiple scales and multiple species, to fully discern how the landscape might influence productivity.

Aside from estimating nest success, the other critical component to assessing productivity for a shorebird is chick survival. Many studies have shown that measuring nest success alone is not a complete metric for understanding overall reproductive success (Cohen et al. 2009), and that nest survival is often less important than chick survival in increasing populations (Dinsmore et al. 2010). Studies have shown that habitat characteristics, environmental factors, and risks from predators or tidal overwash are known to influence shorebird chick survival and rates of fledging success (Cohen et al. 2009, Brudney et al. 2013, Catlin et al. 2013). While multiple studies have focused on chick survival for American oystercatchers (Nol 1989, Davis et al. 2001, Sabine et al. 2006, Collins et al. 2016), few have quantitatively assessed survival rates for Wilson's plover chicks (Ray 2011, DeRose-Wilson et al. 2013). Both species take more than a month from the time of hatching until they fledge, when they are capable of controlled, independent flight (Corbat and Bergstrom 2000, Nol and Humphrey 2012). During this time they are highly vulnerable, however in some cases management actions have been shown to be highly effective for increasing success (Dinsmore et al. 2010), and therefore further study of chick survival is warranted.

Research focused on the factors that influence productivity is becoming more relevant as environmental changes exacerbate stress on beach-nesting shorebirds. Increased recreation and other disturbance, and development of habitat can limit nest sites and reduce productivity (George and Schweitzer 2004, Sabine et al. 2006, Brown 2013), but even relatively undeveloped, pristine habitat like the Georgia barrier islands are subject to changes that result in increased risk of mortality. Two emergent threats that are likely to influence Wilson's plovers and American oystercatchers nesting in Georgia involve increasing risk of predation and tidal overwash of nesting sites. While numerous studies have considered predation risk to be important, several highlight that changes in the assemblages of predators can have a pronounced impact on nesting shorebirds (Hackney et al. 2013). Species that benefit from human dominated landscapes, such as raccoons (*Procyon lotor*), fish crows (*Corvus ossifragus*) and gulls (Family Laridae) have become increasingly common in some regions (Garrott et al. 1993, Martin et al. 2010). Additionally, non-native predators are a serious concern as well; on the Georgia barrier islands coyotes (*Canis latrans*) have expanded their range and have become a significant threat to nesting shorebirds. Tidal overwash has also been shown to decrease nest success; while this risk is not a new threat, factors such as sea level rise, increased unpredictability and intensity of storms, and changing rates of shoreline accretion or erosion (Revell et al. 2011) could have serious implications for nesting shorebirds. Habitat loss has been projected for other beach nesting species as sea levels encroach on open beach habitat (Aiello-Lammens et al. 2011, Sims et al. 2013, Hunter et al. 2015).

Therefore, understanding how these emergent threats might influence productivity of Georgia's shorebirds now and into the future will be important for sustaining populations.

DISSERTATION STRUCTURE

The following chapters have been formatted as manuscripts, and will be multi-authored documents submitted for publication in scientific journals.

In Chapter 2 of this dissertation, we assessed the factors that predicted habitat selection and nest success for American oystercatchers and Wilson's plovers, and determined if both nest-site selection and nest success were influenced by the same habitat features for both species. We also determined how nest-site selection and success varied between the two species. Last, we investigated whether spatial scale influenced how habitat features predicted both nest-site selection and nest success.

In Chapter 3, we assessed how predation and overwash influenced nest success of the Wilson's plover and determined if habitat variables influenced those risks. Specifically, we examined how emergent threats of a non-native predator, the coyote, and shoreline changes due to sea level rise might impact the success of this species by employing competing risks models. We also incorporated rates of shoreline change into our models, and we briefly discussed future applications for the intersection of coastal geomorphology and management of shorebirds.

In Chapter 4, we estimated daily chick survival rates, as well as rates of fledging success for Wilson's plover chicks. We also investigated the influence of several biotic and abiotic variables on survival, and discussed the implications of predation pressure from coyotes on overall productivity for this species.

Finally, in Chapter 5, we discussed the overall implications of these findings and propose avenues for future research. We also applied these findings to the suggestion that American oystercatchers could serve as an umbrella species for Wilson's plovers and other beach-nesting species, and suggested some benefits of multi-species management.

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CHAPTER 2

SITE SELECTION AND NEST SURVIVAL OF WILSON'S PLOVERS AND AMERICAN OYSTERCATCHERS IN GEORGIA: CONSERVATION IMPLICATIONS OF A MISMATCH IN A CHANGING ENVIRONMENT[1]

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[1] Sterling, A. V., J. L. Hatt, T. Keyes, J. Hepinstall-Cymerman, and R. J. Cooper. To be submitted to *The Condor*.

ABSTRACT

Nest site selection is an important component of breeding ecology for all birds, but beach-nesting shorebirds, which use a restricted and specific habitat, face multiple significant challenges. We used a multi-scale modeling approach to determine habitat features that best predict nest site selection and daily survival of nests for American Oystercatchers (*Haematopus palliatus*) and Wilson's Plovers (*Charadrius wilsonia*), two species of conservation concern that nest on the Georgia coast, USA. We found that the same habitat features were not predictive for both species, but an intermediate spatial scale was more informative than the microhabitat features around a nest. Additionally, our results pointed to a potential mismatch between habitat cues used for nest site selection and those that were predictive of daily nest survival for both species, which could indicate that these sites are acting as an ecological trap and have significant conservation implications. These results also highlight the importance of a multi-species approach when determining management goals for this region. This research can be used to direct conservation management to areas of high nest site selection and highly productive areas using habitat features, which will help increase efficiency of management and overall productivity for American Oystercatchers and Wilson's Plovers nesting on the Georgia coast.

INTRODUCTION

For many species of beach-nesting shorebirds (Order Charadriiformes), populations have been declining significantly since at least the 1970s, despite conservation efforts (Brown 2001, Morrison and Johnston 2001). Significant threats to population growth include loss of nesting habitat from development and sea level rise, increased predation threats, and human disturbance (Brown et al. 2000). Although these threats affect many species, beach-nesting shorebirds are particularly vulnerable because this group relies on such a restricted and specific breeding habitat (Brown et al. 2000). Conservation plans directed at maintaining population status highlight the importance of habitat protection and management throughout species' ranges (Brown 2013). However, understanding habitat selection and the influence it has on reproductive success is complicated, especially when multiple species are considered (Misenhelter and Rotenberry 2000), and managers must incorporate both habitat use and reproductive information into conservation planning.

A number of studies have investigated various aspects of shorebird nest site selection, breeding ecology, and reproductive success and point to a non-random distribution of nests, indicating that there may be several adaptive forces exerted on birds as they attempt to determine a suitable nest site (e.g.,Page et al. 1985, Burger 1987, Brown and Brindock 2011, Ray 2011, Gómez-Serrano and López-López 2014). Habitat choice influences reproductive success, and therefore nest-site selection that maximizes an advantage to the individual should be apparent, especially in heterogeneous landscapes (Martin 1995, Misenhelter and Rotenberry 2000, Jones 2001, Robertson and Hutto 2006, Arlt and Part 2007). Because of these forces, habitat selection and the comparative quality of a habitat have been shown to be correlated in some cases (Kellner et al. 1992, Misenhelter and Rotenberry 2000). Individual traits may be adapted to features in certain selected sites, such as having cryptic plumage which would decrease detection by predators (Martin 1998). Additionally, physical features at selected sites could provide an advantage, such as choosing heavily vegetated areas to provide protection for nests

(Powell 2001). Despite the advantages that exist at a given site, there are reasons that individuals may not always select habitat that increases success: for example, social interactions, such as competition, (Vanhorne 1983, Jones 2001, Kokko and Sutherland 2001, Arlt and Part 2007), or individual traits such as site-fidelity. Additionally, several complicating factors can make it difficult to link site selection with reproductive success including (1) mismatches between habitat cues and success due to tradeoffs or changing environmental threats, (2) issues of scale, and (3) requirements that vary by species utilizing the same nesting sites.

Mismatches between habitat features and areas of high nesting success could occur when individuals are not able to perceive the physical cues that are present at a site, or those cues may not actually be informative (Kokko and Sutherland 2001). Rapid habitat changes can decouple the environmental cues that an individual uses to assess perceived habitat quality with true habitat quality, which can lead to ecological traps (Kokko and Sutherland 2001, Schlaepfer et al. 2002, Battin 2004). These changes can be large scale changes, such as sea-level rise due to climate change or biotic changes to a nest site (Harding et al. 2001, Sims et al. 2013). However, even when habitat cues are informative for an individual making habitat choices, the decision can be complex because features might represent trade-offs that influence overall success. This has been demonstrated for various species of beach-nesting birds. In some cases, nest sites are located near vegetation, which provides relief from environmental extremes and protection from avian predators, although areas of dense vegetation can also provide shelter for mammalian predators, which could increase risk (Burger 1987). Similarly, nests observed in close proximity to anthropogenic or natural objects on the beach may receive protection from avian predators. However, these objects may also act as markers for mammalian predators; researchers conducting a study of Snowy Plovers (*Charadrius nivosus*) noted that they used objects on beaches as cues to locate nearly a third of the nests in their study (Page et al. 1985). It has also been shown that objects or vegetation may decrease the ability of some birds to perceive predators by limiting visual detection (Brown and Brindock 2011, Gómez-Serrano and López-López 2014). These tradeoffs underscore the importance of understanding how both biotic and abiotic features influence nest site selection as well as nesting success for beach-nesting shorebirds (Ray 2011).

Additional complexity quantifying habitat selection occurs because there is variation in habitat features at different spatial scales within a landscape, which influences both habitat use and the distribution of individuals (Turner 2006, Crampton and Sedinger 2011, Chandler and Hepinstall-Cymerman 2016). Birds make habitat choices based on information from multiple spatial scales, and to fully understand habitat selection and productivity, we need to incorporate variation across spatial scales (Jedlikowski et al. 2016). Johnson’s order of selection provides an ideal framework for investigating habitat selection hierarchically, and has been applied often to shorebirds where first order selection focuses on habitat, second order selection focuses on territories, and third order selection focuses on nest sites (Johnson 1980, Burger 1987). Factors influencing nest site selection can include micro-habitat characteristics, such as substrate choice or density of surrounding vegetation (Lauro and Burger 1989, Corbat 1990, Powell 2001, Brown and Brindock 2011), macro-habitat characteristics, such as proximity to water, tide line, dunes, or mud flats (Burger 1987, Nol 1989) or features from multiple spatial scales working in concert (Bergstrom 1989, Ray 2011). These factors will influence reproductive success by affecting, among other things, vulnerability of eggs and offspring as well as protection from various biotic factors. Scale can also effect some of the other complicating factors of habitat selection; for example an ecological trap could exist at the nest-site scale and not at the territory scale (Misenhelter and Rotenberry 2000) or could influence trade-offs. Therefore, it is important to incorporate variables from multiple spatial scales when assessing how habitat selection might influence nesting success.

We focused this study on two co-occurring species of beach-nesting shorebirds to investigate how nest site selection correlates with the success of nests for each species individually, but also how these relationships might differ between species. At our study sites, both Wilson’s Plovers (*Charadrius wilsonia;* WIPL) and American Oystercatchers (*Haematopus palliatus;* AMOY) and have similar life-history traits and nesting strategies (Schneider et al. 2010). Both species select, maintain, and defend nesting territories throughout the season, locating nests within these defined territories once they are established (Corbat and Bergstrom 2000, George 2010). However there are some differences in nesting behavior and morphology that could lead to divergent nesting requirements (Martin 1998). If significant size differences between the species, behavioral differences regarding nest defense, or preferences for different habitats exist, species could face different risks during nesting. Additionally, these species could respond to the complicating factors of mismatches and scale differently; for example behavioral plasticity might influence responsiveness to ecological traps (Kokko and Sutherland 2001), and body size or territory size might impact how scale influences habitat selection (Jaenike and Holt 1991). However, we do not know the degree to which these differences between species might translate to differing habitat requirements, and differing rates of success. Therefore, understanding the interactions between nest site selection and success for each species is important for managing both threatened species.

The American Oystercatcher and Wilson's Plover have been designated as species of high regional conservation priority by the US Shorebird Conservation Plan and within the Atlantic Flyway (Brown 2001, Brown 2013); within Georgia, the American Oystercatcher is listed as rare while the Wilson's Plover is listed as threatened (GADNR 2015). Current management in Georgia is focused on protection of areas of high nesting density, however to improve productivity, it may be beneficial to identify and then shift the focus to areas of high nesting success. Across the East Coast and within Georgia, a significant amount of shorebird conservation and management actions have focused on American Oystercatchers. It has been suggested that this species also serves as an umbrella species, and that management focused on increasing success for American Oystercatchers may also benefit other beach-nesting birds such as Wilson's Plovers (George and Schweitzer 2004). However, little is known about fine and large-scale habitat features that predict nest site selection and nest success for Wilson's Plovers, despite the overlapping range with larger and well-studied American Oystercatchers. With this research, one objective was to understand how habitat features influence each species' site selection and reproductive success to determine if management objectives should be modified to more fully incorporate conservation goals for Wilson's Plovers.

The specific objectives of this study were to: (1) Assess the factors that predict habitat selection and nest success for American Oystercatchers and Wilson's Plovers, and determine if both nest-site selection and nest success are influenced by the same habitat features for both species. Due to selection pressure, we predicted that there would be a correlation between site selection and reproductive success. (2) Determine how nest-site selection and success vary between the two species. We hypothesized that because both species had similar nesting requirements on barrier island beaches, the same features would influence nest-site selection and nest success for both American Oystercatchers and Wilson's Plovers. (3) Determine if spatial scale influences how habitat features predict both nest-site selection and nest success. Our third hypothesis was that, although the two species would be using the same habitat features within a given spatial scale to select nest sites and those features would be predictive of nest success, the spatial scale best predicted by habitat features would vary by species. For this study, we chose to incorporate variables at two spatial scales that we predicted would be biologically informative and relevant, but also easily identified by managers to increase the applicability of these results. By determining what habitat features from the most informative spatial scale influence nest location and nest success, we can ultimately guide conservation management to increase productivity for both species.

METHODS

Study Sites

During the 2012 and 2013 breeding seasons, from mid-March until late July, we monitored two sites that were comprised of three barrier islands with previously detected populations of breeding Wilson's Plovers and American Oystercatchers (Corbat 1990, George and Schweitzer 2004, Sabine et al. 2006). Little St. Simons Island (LSSI; ca. 31.26°N, 81.27°W; 5,260 ha) is a privately owned, undeveloped barrier island located in

Glynn County at the southern branch of the Altamaha River Delta (Figure 2.1). It has approximately 11 km of wide, ocean-front beach with areas of tidal overwash, preliminary and well-developed dunes with moderate vegetation, and areas of marsh ponds. There are two tidal creeks that bisect the beach to the Atlantic Ocean, and areas of marsh and mudflats that are accessible from the beach front. Cumberland Island National Seashore (CUIS; 30.85°N, 81.43°W; 14,736 ha), has approximately 29 km of beach, however we focused our efforts on the 4 km stretch of northern beach known as Long Point. Included in this site is Little Cumberland Island (LCI; 30.97°N, 81.41°W; 2,300 ha), which is privately owned and separated from the larger island by a tidal creek. Both LSSI and CUIS have wide beaches and well-developed dunes and serve as critical nesting areas for shorebirds, sea birds and sea turtles (Schneider et al. 2010). Importantly, these are dynamic habitats with areas of both significant erosion and accretion, and a tidal amplitude of nearly 3 meters (Davis 2004, Jackson 2010). They are generally composed of heterogeneous plant communities, including active primary dunes dominated by sea oats (*Uniola paniculata*) and beach elder (*Iva imbricata*) and overwash areas dominated by railroad vine (*Ipomoea pes-caprae*) and sea purslane (*Sesuvium portulacastrum*) (Duncan 1982, Schoettle 1984). The back-dune areas at these sites range from areas of dense *Spartina patens*, mud flats dominated by *Salicornia spp.*, and marsh dominated by *Spartina alterniflora*.

Nest Searching and Monitoring

Nests were located through behavioral observations of adults, following tracks, and through systematic searches of all available nesting habitat (Powell 2001). Both sites were divided into thirds and we searched each section every third day to ensure adequate and even coverage and reduced disturbance. Once found, locations of nests were recorded using Garmin GPSMAP 60CSx handheld units and monitored every three days throughout incubation. If a Wilson's Plover nest was found after clutch completion (three eggs in nest, or two checks of only one or two eggs), eggs were floated to determine their approximate lay date to aid in banding of chicks for a different study (see Chapter 2; Hood 2006). American Oystercatcher eggs were not floated because chicks were not banded at hatching. A fate was assigned as either successful, when at least one egg hatched, or failed. Nests with unknown fates were censored from this study. When a nest failed, we determined cause of failure, if possible, by observing any evidence, such as predator tracks, egg shells or debris, and the state of the nest cup for signs of flooding. When a failed nest was not washed over, but no definitive predator could be assigned, the cause of failure was listed as 'predator unknown.'

Every effort was made to minimize disturbance. Nest searching and monitoring were carried out in each section of beach once every three days unless temperatures exceeded 100°F, winds exceeded 20 mph, or if heavy rain was falling. Due to these extraneous factors, if a beach section was missed on the scheduled day, monitoring resumed as soon as conditions permitted.

Habitat Variables

We categorized biotic and abiotic characteristics at two spatial scales: microhabitat and macrohabitat, which approximately correspond to the scales of selection of a nest-site and a territory, respectively (Burger 1987).

Microhabitat. Once nests were no longer active, a marked wooden dowel was placed in center of the nest cup to mark the elevation. At the conclusion of the nesting season, we measured the elevations of all nests referenced to the marked elevation, using Real Time Kinematic (RTK) satellite navigations GPS (Trimble5800, Trimble Navigation Limited, Sunnyvale, CA; +/-1-2cm accuracy). Nest elevation is an important characteristic that affects flooding probability and different species may vary in their tolerance of flooding risk (Corbat 1990, Rodrigues 1994, Anteau et al. 2012). We also measured several microhabitat characteristics within a one-square meter quadrat which was centered on the nest. We recorded ocular estimates of the percentage of substrates, which were classified as open sand, shell, wrack, or vegetation, which can influence crypsis of eggs and chicks thereby affecting survival (Page et al. 1985, Corbat 1990, Hood 2006). We also recorded all plant species within the quadrat and recorded if the nest cup was located within the vegetation (if more than 50% of the nest cup was surrounded by vegetation). Vegetation at the nest may influence overall success as it could provide cover, act as a windbreak, or may limit the ability of incubating adults to detect predators (Bergstrom 1988, Corbat 1990, Hood 2006, Brown and Brindock 2011, Ray 2011, Nol and Humphrey 2012). For every nest site measured, a comparable random site was also characterized using the same set of parameters to assess an unused site for comparison. Random nest sites at the microhabitat scale were located within 25 meters of the original nest site to ensure they were within the same territory, and were chosen using a random number table to determine compass-degree direction and distance from the original nest. If the random site fell below the mean high tide line, or in the marsh, a new random number combination was selected.

Macrohabitat. To quantify habitat features at the intermediate territory-scale, we incorporated the surrounding community composition and the distance to habitat features for each nest site. We used a 25-meter radius buffer to approximate an individual bird's territory size, although we recognize that territories are variable based on habitat quality, individual variation, and composition of the landscape (Schulte et al. 2010, Zdravkovic 2013). To assess community composition, we used a fine-scale map of the study sites, hand digitized from a 2012–2013 Coastal Georgia digital aerial orthorectified 4-Band 6-inch pixel imagery, at a map scale of 1:300 to 1:500 resolution to categorize the landscape into distinct communities (Geiss 2010). Communities were differentiated based on the literature and knowledge of the sites and included geomorphic features and the presence of distinct plant species to distinguish unique communities (Duncan 1982, Schoettle 1984). This approach resulted in a total of 15 unique cover types (Table 2.1), which were ground-truthed using 100 points randomly distributed across the study site and were verified as 82% accurately classified. Given the highly dynamic nature of the study sites, we are confident that this classification accurately represents the landscape, however it is limited in temporal application. Including these unique communities as variables allowed for more fine-scale identification of habitat types than previously available habitat maps provided, while being broad enough that the types are readily apparent to observers and managers. We then identified the percentage of different community types that were located within a 25-meter radius circle around each nest to approximate the territory size using spatial analyst tools in ArcGIS (ESRI 2011). Four of the most prevalent community types, in order of their dominance, were "active dunes", "interdune meadow", "overwash beach", and "open beach". These community types were used as variables in our models, with the remaining 11 community types combined into the “other” category, as they comprised less than 4% of habitat around the nests (Table 2.1).

Using the same imagery, we also measured distance from each nest location to several habitat features including tide line, marsh edge, and edge of upland areas using the Euclidean Distance tool in ArcGIS (ESRI 2011). We expected the proximity to these features to influence nest survival. For example, edge effects in forests and grasslands have been shown to increase predation risk to nests and these effects may also apply to beach nesting birds as well (Paton 1994). Upland areas may provide a source of predators, which could affect nest site selection and daily survival of nests (Lima 2009, Pruner 2010), while distance to tideline and marsh edge might influence flooding risk.

To compare chosen sites with available habitat, random sites were generated from a systematic array of points across the landscape created using the Fishnet tool in ArcGIS. These points were positioned at 50-meter intervals to allow us to sample the communities at a 25-meter radius buffer for each point (Figure 2.2) and prevent overlap. These points were restricted to nesting habitat (excluding marsh, upland and areas below the tideline) and adequately represented the available habitat from which birds were able to choose (Benson and O'Hara 2013).

Analytical Methods

We used logistic regression to estimate the probability of a nest site being selected as a function of the variables measured at the two spatial scales. Our models were built using general linear models where we specified a logit link function to restrict the response variable (site not selected or selected) to probabilities between 0 and 1. To estimate daily survival of a nest and investigate which covariates influenced nest success, we used logistic-exposure models which account for variation in exposure days between nest visits, and allows for different survival rates between nest checks (Shaffer 2004). Here, the response variable is survival, and again the logit link function restricts the probability of survival between 0 and 1 (nest failed or survived). All of the covariates in the models we created were treated as fixed effects, to allow for convergence of models and model ranking. Identical sets of models were built for both species and all models were ranked at both spatial scales using Akaike's Information Criterion corrected for small sample size (AIC_c; Burnham 2002) to determine the support for influential habitat features at each scale. Top models (within $\Delta 2$ AIC_c) from each scale were then combined and ranked again to determine which scale was best supported, for each species.

First, for the microhabitat scale, we tested the effect of a categorical variable (nest located in vegetation/not) and several continuous variables (percentage of substrate types, elevation) on nest location and survival by ranking an exhaustive set of additive models including a global and null model for each species. This resulted in a total of 35 models for comparison. Next, we evaluated nest site selection and survival at the macrohabitat scale with models that included the habitat composition (as percentage of the top four community types as well as the "other" community type) that comprised the 25-meter buffer around the nest site. We ranked the community models first, and then incorporated the effects of proximity to habitat features (distance to tide line, distance to marsh edge, distance to upland edge) to the top set of community models, to reduce over-parameterization. Then we ranked the combined community and feature models to determine how nest location and daily survival were influenced by variables at the macrohabitat scale.

All continuous variables were centered and scaled, and tested for correlation using the Pearson correlation test. Variables with $r \geq 0.7$ were removed from this analysis (Dormann et al. 2013). The only variables that were correlated were percentage of vegetation and percentage of open sand within one-square meter of the nest at the microhabitat scale. We retained the variable of percentage of open sand to reduce redundancy as we also included the categorical variable of nests located in vegetation. For all sets of models we included year and site as categorical fixed effects to account for differences between study sites and years, and all model sets included both a global and a null model for comparison.

We considered the models from each scale competitive if they were within Δ2 AIC_c units of the best model (i.e., lowest AIC_c score), and these were used for a final comparison of both scales. While we recognize that including all models within Δ2 AIC_c of the top model includes models with uninformative parameters (Arnold 2010), we wanted to be less conservative and carry the greatest number of models forward from both spatial scale. We compared the competitive set of models from each scale to the other to determine which scale was the most informative overall. We were able to directly compare the nest survival models from both scales using AIC_c to rank a set of models that included the microhabitat and macrohabitat features, as well as a global model with all variables included and a null model for comparison (Figure 2.3). For the nest site selection models, the microhabitat models compared selected nest sites to unused random sites, whereas the macrohabitat models compared used sites to available habitat, so the two scales could not be directly compared. Therefore, we assessed model fit of the site selection models using a *k*-fold cross validation, which is relevant for used versus available habitat selection analyses (k-folds=10; Boyce et al. 2002), for both the microhabitat and the macrohabitat models to determine which scale was most informative (Figure 2.4).

Finally, we used the top model or set of models to predict how nest location and daily survival would be influenced by the significant variables, which were considered significant if their confidence intervals did not include zero. If there were multiple competitive models, we model-averaged them to obtain parameter estimates. We also estimated daily nest survival from the top survival model for each species, and nest-period survival was calculated as well. For Wilson's Plovers, we based nest-period survival on a 25-day incubation period (Zdravkovic 2013) and for American Oystercatcher we based it on a 28-day incubation period (Nol and Humphrey 2012). All statistical analysis were conducted in Program R (R Core R Development Core Team 2015) and we present all summary variables as means +/- standard errors (SE).

RESULTS

We located a total of 429 Wilson's Plover nests and 58 American Oystercatcher nests during the 2012 and 2013 field seasons. In 2012, we found 211 Wilson's Plover nests, of which 97 were on LSSI and the remaining 115 were located on CUIS and LCI. In 2013, we found 115 nests on LSSI and 103 on CUIS and LCI for a total of 218 Wilson's Plover nests for the year. We found 23 American Oystercatchers nests in 2012, with 17 located on LSSI and 6 located on CUIS. In 2013, we found 35 nests, with 21 located on LSSI and 14 nests on CUIS. These totals include renesting attempts over the course of the breeding season, however because the adult population is not marked with color bands, we had no way to accurately assign nests to individuals. Therefore, some pseudoreplication is present in our data. More specifically, both species renest following a nest failure, but seldom renest more than three times in a season, and in Georgia there have been no reports of renesting after successful fledging of chicks (Corbat and Bergstrom 2000, Zdravkovic 2013). We monitored Wilson's Plover nests every 2.65 ± 0.03 days for a total of 1,791 observations in our survival models and monitored American Oystercatcher nests every 2.68 ± 0.06 days for a total of 332 observations. The primary causes of nest failure for observed nests were predation and overwash for both species; 56.2% of Wilson's Plover nests were depredated while 13.3% were overwashed, and 65.5% of American Oystercatcher nests were depredated and 12.1% were inundated.

Nest Site Selection

Microhabitat Scale. *Wilson's Plovers:* At the microhabitat scale we compared nest sites to paired, randomly located unused sites, and had a total of 860 locations in this analysis. We found that the model that best predicted nest site selection of Wilson's Plovers was the global model (Table 2.2), which included all covariates including percentage of wrack cover, the percentage of openness, the percentage of shell cover, elevation, the categorical variable of nest location in vegetation as well as site and year. There were 3 of 35 additive models that were within 2 ΔAIC_c units of the top model, which we model averaged to determine effects of the parameters on site selection (those with confidence intervals that did not overlap zero). We found that the percentage of wrack cover, elevation, and vegetation at the nest site had a positive effect on nest site selection (Table 2.3). The percentage of openness had a negative effect on site selection.

American Oystercatchers: We compared used nest sites selected to unused nest sites, which created 116 locations for American Oystercatchers. At the microhabitat scale, the best model included the percentage of wrack cover, which had a positive effect on nest site selection, and the percentage of openness around a nest sand, which had a negative effect on site selection, as well as site and year (Table 2.3). There were 4 out of 35 models that were within 2 ΔAIC_c units of the top model and these were all advanced to the final multi-scale model for selection (Table 2.2).

Macrohabitat Scale. *Wilson's Plovers:* We compared features at chosen nest sites with the available habitat using a total of 2827 systematic points to represent the available nesting habitat. After combining and ranking both the community models and the feature models, the best model for Wilson's Plovers included the percentage of open beach, the percentage of other community types, the distance to upland and the distance to the tideline, as well as site and year. There were five models that were ranked within 2 ΔAIC_c units of the top model for Wilson's Plovers (Table 2.2), which we model averaged to obtain parameter estimates. Parameters with confidence intervals that did not include zero were the percentage of open beach, percentage of other community types and distance to tideline, which negatively influenced nest site selection and distance to upland, which positively influenced nest site selection (Table 2.4).

American Oystercatchers: The top model for nest site selection for American Oystercatchers included the percentage of active dunes, the percentage of overwash beach and the percentage of other community types, and the distance to all three habitat features (upland, tideline and marsh), as well as site and year. There were six models that were within 2 ΔAIC_c units of the top model (Table 2.2). When we model averaged these top models, the parameters with confidence intervals that did not include zero were the percentage of active dunes, the percentage of overwash beach, and the distance to upland, which positively influenced nest site selection. Distance to the marsh edge, and distance to the tideline negatively influenced nest site selection (Table 2.4).

Scale Comparison. Using *k*-fold cross validation, we compared the goodness of fit for the top microhabitat model with the fit of the top macrohabitat model for both species, because we could not directly compare the two scales given our spatial data. The top microhabitat model for Wilson's plovers predicted site selection correctly 66.47% of the time, while the top ranked macrohabitat model showed better fit at correctly predicting site selection 89.86% of the time. For American Oystercatchers, the model from the macrohabitat scale had a marginally better fit (70.06%) than the top model from the microhabitat scale (69.35%). We plotted variables from the most informative spatial scale to visualize how the habitat features influenced nest site selection for both Wilson's Plovers (Figure 2.5) and American Oystercatchers (Figure 2.6).

Nest Survival

Microhabitat Scale. *Wilson's Plover:* The best ranked survival model for Wilson's Plovers at the microhabitat scale included the percentage of openness and the percentage of wrack cover as well as site and year. We advanced 5 out of 35 models that were within 2 ΔAIC_c units of the top model to the final set of multi-scale models (Table 2.5). We model averaged the top models to determine the influence of parameters with confidence intervals that did not include zero. Aside from site and year, the only habitat feature that influenced nest survival at this scale was the amount of openness around the nest, and it had a negative effect, however the effect size is very small (Table 2.6).

American Oystercatcher: The best ranked model for nest survival of American Oystercatchers included the presence of vegetation around the nest as well as site and year. We advanced 7 out of the 35 models that were within 2 ΔAIC_c units of the best model, including the null model of site and year, to the multi-scale modeling stage (Table 2.5). After model averaging the top set of models, the only parameter that had confidence intervals that did not include zero was site, and the effect sizes for all parameters from the candidate set of models were very small (Table 2.6).

Macrohabitat Scale. *Wilson's Plover:* At the macrohabitat scale, the covariates that best predicted nest survival for Wilson's Plover were the percentage of the active dune community, the percentage of the overwash beach community, the percentage of other community types and the distance to upland, as well as site and year. We included the 7 out of the 32 models that were within 2 ΔAIC_c units of the top ranked model in our final set of multi-scale models (Table 2.5). We model averaged these, and found that, in addition to site and year, the percentage of overwash beach and the distance to upland influenced nest survival negatively, although both effects were very small (Table 2.7).

American Oystercatchers: For American Oystercatchers, the top ranked model for nest survival included distance to the tideline, site, and year. We included this model and the next 9 out of 26 models that fell within $\Delta 2AIC_c$ units in our final multi-scale set of models (Table 2.5). The model averaged parameter values indicated that the habitat features we included had little effect on nest survival, and all included zero within the confidence intervals, with the exception of site (Table 2.7).

Scale Comparison. To determine which scale is more informative we ranked the top models (those less than $\Delta 2AIC_c$ units) from the microhabitat and the macrohabitat scales. For Wilson's Plovers there were 7 out of 17 models that were competitive, but only the top two models included no uninformative parameters (Table 2.8; Arnold 2010). These top two models were from the macrohabitat scale, and the community types of open beach and interdune meadow had a positive effect on nest success, while the percentage of overwash beach and the distance to the upland negatively influenced nest success (Table 2.9; Figure 2.7). We used the top model to predict a daily survival estimate for Wilson's Plover nests of 0.93 (95% CI 0.91–0.95) and calculated a nesting period survival of 0.17 (95% CI 0.10–0.26).

After combining and ranking the survival models from both spatial scales, we had two competitive models for American Oystercatchers that ranked ahead of the null model (Table 2.8). The microhabitat scale model that included the effect of a nest being located in vegetation and the landscape scale model which included the variable of the distance to the tideline were model averaged, but the only parameter that was informative was site (Table 2.9). Both habitat variables, as well as year, had confidence intervals that overlapped zero, indicating that the habitat features we measured were not informative in predicting nest success. We used the top model to calculate a daily survival estimate for American Oystercatcher nests of 0.94 (95%CI 0.90–0.97) and a period survival estimate of 0.21 (95%CI 0.05–0.44).

DISCUSSION

The relationships between habitat features, nest site selection, nest success, scale, and the requirements of different species are complex and variable, and we need to better understand how these factors interact to successfully conserve beach-nesting shorebirds. We expected that the features predicting nest site selection would also predict nest success, however, our results showed that there was very little overlap for both Wilson's Plovers and American Oystercatchers. The mismatches that we found between selection of nest sites and nest survival could be due to several processes. We also saw that the habitat features that predicted nest site selection and nest success varied between the two species and that site selection and nest success also varied by scale. These results highlight that there are risks to basing conservation management decisions solely on habitat features alone, and adding multiple factors when examining nest site selection and success is critical.

Wilson's Plovers and American Oystercatchers both chose nest sites with habitat features that could provide an advantage, and despite a large amount of variability, some of the patterns that we saw are also well supported in the literature. At the microhabitat scale, Wilson's Plovers chose sites with more wrack, higher elevation and located within vegetation. Nests were less likely to be located in open sand areas. These patterns have been observed in other studies of Wilson's Plovers in Georgia, North Carolina, and Texas, where vegetated nest sites may provide cover, thereby increasing nest success (Bergstrom 1988, Corbat 1990, Hood 2006, DeRose-Wilson et al. 2013). At the macrohabitat scale, territories were more likely to be located farther from upland areas, closer to the tideline, and were less likely to be located in the open beach community or the 'other' community type. Upland and open beach areas could increase predation risk for birds by, respectively, providing refugia for mammalian predators and reducing cover for nests (Pruner 2010). For American Oystercatchers, nests were more likely to be located at sites with more wrack, and also were less likely to be located in areas of open sand. This has been documented in previous studies in Georgia and New York (Lauro and Burger 1989, George 2002). Territories were more likely to be located in the active dunes and overwash sites, farther from the upland, closer to the marsh and closer to the tideline. This could influence both the risks from predation and tidal overwash. Site was an informative variable for both species, and variation between sites and throughout the breeding range has been noted for American Oystercatchers and Wilson's Plovers (Lauro and Burger 1989).

Despite the apparent benefits of the habitat features that best predicted nest location, they were not the same features that predicted nest success. The most informative survival models for each species included features that were either different or in some cases, contradictory to the site selection models. For Wilson's Plovers, there was only one feature that was predictive of both site selection and survival at the microhabitat scale, which was the amount of openness around the nest. This indicates that openness around the nest may actually be an informative habitat feature for selecting successful nest sites, although the effect size was very small for the survival models. However, at the macrohabitat scale, as the distance to upland increased there was increased probability of selection, but a decrease in survival. This type of mismatch could have serious implications, as birds may be selecting sites that are riskier due to predation or some other factor. For American Oystercatchers, there were no habitat features that were predictive of nest survival, aside from site. The features useful for predicting site selection were not informative in the nest survival models. Previous studies focusing on nest survival for American Oystercatchers have also found habitat features to be a poor predictor of nest success (Corbat 1990).

When features that are predictive of nest site selection do not reflect features that predict high rates of survival, as we saw at our study sites, this could be an indication of an ecological trap. This occurs when conditions or threats within an environment have changed and habitat features are no longer informative cues for individuals (Schlaepfer et al. 2002, Anteau et al. 2012). Ecological traps have been documented to affect a wide range of taxa. They have been shown to influence nest survival in grassland systems, where birds preferentially nest in pastures of a specific structure but experience reduced success due to farming activities (Best 1986). Negative edge effects, where birds selecting nest locations because of structural habitat cues along edges become more vulnerable to predation or parasitism, are also sometimes considered ecological traps (Paton 1994). While ecological traps are most commonly documented in avian and insect systems (Schlaepfer et al. 2002), they have been identified for other taxa as well. West Indian Manatees (*Trichechus manatus*) in Florida utilizing warm water discharge from power plants can become stranded in cold water after incorrectly identifying habitat cues (Packard et al. 1989), and snapping turtles (*Chelydra serpentin*) in Illinois have been documented to incorrectly perceive habitat cues in areas of high human development which leads to decreased nest success (Kolbe and Janzen 2002).

Habitat features may not reflect high quality nest sites for shorebirds in our study due to several emergent threats. Changes such as rising sea levels, which influence the risk of tidal overwash of nests (Sims et al. 2013), and increased abundance or changing assemblages of predator communities, which influence depredation rates (DeRose-Wilson et al. 2013, Ringelman 2014), may reduce the effectiveness of habitat features as cues for nesting shorebirds. Changes in habitats can alter the cues that individuals depend on for making decisions with or without altering the overall suitability of a landscape (Robertson and Hutto 2006). Therefore, even at our relatively pristine study sites, habitat attractiveness may not be changing but because of some risk, such as increased tidal inundation threats or novel predators, previously suitable sites may no longer be successful. Because cues are not necessarily changing there is still an equal chance of selection among these habitat features, but the outcome might be altered, leading sites to function as ecological traps (Robertson and Hutto 2006).

Additionally, other processes might influence the mismatch we observed in our system. In comparison to other studies, nest success is low at our study sites; however, nest success alone may not be a good indication of habitat quality. Tradeoffs may also be an important component to nest site selection, and these should be examined to understand whether habitat selection is truly adaptive (Misenhelter and Rotenberry 2000). For instance, Wilson's Plovers were more likely to locate nests in vegetation, which could reduce the risk of adult mortality or reduce adult exposure, but dense vegetation was not predictive of nest survival. However, dense vegetation might influence some other demographic measure of success (such as adult or fledgling survival) instead of nest survival. Or dense vegetation might influence an individual's food availability or ability to fledge chicks. Additionally, some shorebirds have shown significant plasticity and flexibility in regard to nest site selection, suggesting that they may be able to adapt well in the face of rapidly changing habitat (Page et al. 1985, Lauro and Burger 1989, Cohen et al. 2009). At our site, birds may be adapting to new habitat cues, but because this study is short in duration and we did not include individual traits, we are not able to detect that shift (Misenhelter and Rotenberry 2000). Regardless of the cause, a mismatch between habitat features predicting site selection and those predicting nest success could imply negative impacts at the population level and in some cases extinctions (Battin 2004);

however the timeframe of this project is too short to make such a determination (Kellner et al. 1992)

Understanding how the mismatches between site selection and nest survival influence productivity for one species is complex, however the complexity increases when multiple species are involved. There was some overlap in features predicting nest site selection between Wilson’s Plovers and American Oystercatchers. At the microhabitat scale, the amount of openness negatively influenced site selection and the amount of wrack positively influenced site selection for both species. At the macrohabitat scale both distance to upland and distance to tideline influenced site selection in the same direction for both species. However, we found that the habitat features that best explained nest survival were not the same for both species. This might be due to niche differentiation or different behavioral or life history traits despite the species nesting sympatrically, which could influence the vulnerability of nests (Corbat 1990, Corbat and Bergstrom 2000, Nol and Humphrey 2012). For example, behavioral differences include nest defense; when threatened at the nest, Wilson’s Plovers exhibit dramatic broken-wing displays (Zdravkovic 2013), while American Oystercatchers generally flee the nest area silently (Nol and Humphrey 2012). Visibility of incubating birds and of nests is greater for American Oystercatchers than it is for Wilson’s Plovers (Schneider et al. 2010). American Oystercatcher eggs are significantly larger than Wilson’s Plover eggs where eggs have a mean length of 56.2 ± 0.3 mm versus 35.2 ±0.1 mm, respectively (Bergstrom 1988, Nol and Humphrey 2012). Additionally, a significantly greater amount of visible disturbance and tracks left at an American Oystercatcher nest site compared to a Wilson’s Plover nest site might also increase detectability. Due to these factors, the two species may experience different levels of vulnerability, which could result in disparate features predicting nest survival for each species.

Differences in life history traits have also been shown to have implications for nest site selection. Long-lived species, such as American Oystercatchers, which typically have a lifespan of ten years but could potentially live as many as 40 years (Nol and Humphrey 2012), tend to exhibit flexibility in habitat selection (Kokko and Sutherland 2001). In addition to nesting on barrier islands, American Oystercatchers also nest on emergent sand spits, shell rakes, and elsewhere in their range there have been reports of nests located on rooftops or on rocky islands (Nol and Humphrey 2012). This flexibility could explain why there was less agreement between features that predicted site selection and nest success for American Oystercatchers compared to Wilson's Plovers. Wilson's Plovers are less long-lived, and therefore, habitat selection may be more influenced by natural selection (Kokko and Sutherland 2001), which could mean that habitat features are better predictors of success for this species. In our study, even though there was greater variability, American Oystercatchers had a higher nesting period survival than Wilson's Plovers, which could indicate that increased flexibility allows for adaptation to novel threats and increases nest survival.

As seen in other systems, scale does appear to be important for predicting both nest site selection and nest survival, especially for Wilson's Plovers. When we compared goodness-of-fit tests of each scale for the site selection models, the macrohabitat had a significantly higher score than the microhabitat scale. The nest survival models at the macrohabitat scale were also ranked higher that the models at the microhabitat scale, indicating that habitat features might be more important for birds in selecting a territory rather that selecting a nest site within the territory. However, for American Oystercatchers, neither scale was better than the other for predicting either nest site selection or nest survival. Despite this, the macrohabitat scale, representing territories, has been shown to be particularly important in other studies as well. Studies of European Oystercatchers (*Haematopus ostralegus*) have shown that territory selection influences overall productivity and this fitness advantage would likely influence site selection in our system as well (Ens et al. 1992). However, the effects of territory quality on nest success can be very difficult to assess without including traits of individual bird quality because factors such as age and parental experience can also influence overall nest survival (Goodburn 1991). The effects of habitat choices, especially the establishment of territories, can also be influenced by population size (Kristan 2003). At our study sites, Wilson's Plovers were more widely distributed across potential nesting habitat than American Oystercatchers, which could explain why habitat features at the territory scale were informative only for plover nest survival and not American Oystercatchers. An increased sample size of American Oystercatchers would allow us to better identify which spatial scale is most informative for predicting the habitat features that influence survival for this species and also allow us to make better comparisons between the two species.

Overall, it appears that habitat features are more useful for predicting nest location rather than nest success for both species. This is especially true for American Oystercatchers because no habitat variables were strongly predictive of nest success. Site and year were predictive of nest success, and because risks to daily survival vary among different temporal and spatial scales, it is critical to base management decisions on the conditions at each site. Variation between site and year is likely a result of external forces, such as tidal events and predation, which have a significant influence on daily survival of nests. In our study, coyotes (*Canis latrans*), which had a significant impact on survival of nests, were present on Cumberland and Little Cumberland Islands but not on Little St. Simons Island. Future studies should investigate how risks change over time at sites to better identify threats and management actions that can ameliorate them (see Chapter 3).

These results suggest that, although managers may not be able to rely on the habitat features that we included in our study to identify the most productive nesting habitat for American Oystercatchers, it may be possible to identify areas of high success for Wilson's Plovers from these features. It is possible that we did not include the habitat cues that American Oystercatchers use to assess habitat quality in our models, which resulted in our inability to identify habitat features that were predictive of success. However, managers should be aware that focusing only on conservation of habitats that are predictive of nest site selection without including areas of high success, could enhance the risk that some of the more productive nesting areas are being missed (Kristan 2003). For example, enhancing the community composition of features that promote nest site selection, such as active dunes, without incorporating features that influence nest success, could promote an ecological trap, which could result in overall reduced productivity. Managers should focus planning efforts at the macrohabitat spatial scale, because this scale produced the models with the best performance, and these features are more readily apparent and easy to identify in the field. The community classification used in this study is at a scale that is relatively easy to assess from remotely sensed data sources, which could be advantageous for planning surveys and predator removal actions.

Currently, the state of Georgia invests significant resources in predator control to increase success of American Oystercatchers, which undoubtedly benefits Wilson’s Plovers. In this regard, the American Oystercatcher does act as an umbrella species, however managers should expand their focus to include Wilson’s Plovers as well. Nest survival models were more informative for Wilson’s Plovers, in part because their higher density led them to saturate the landscape which increased the predictive capacity of our models. Incorporating the modeling results for Wilson’s Plovers into conservation planning will increase efficiency of management and likely increase nest survival rates for many beach-nesting species (Keyes, pers. comm.). More research and analysis is needed that will focus on competing risk models which incorporate habitat features as well as temporal, biotic and abiotic factors as variables to better identify how the risks of tidal overwash and predation influence nest success (see Chapter 3). This will allow us to further investigate the possible mismatch between habitat features that predict nest site selection and variables that predict nest survival, and to plan for how productivity for Georgia’s shorebirds might respond to changing conditions in the future. This study shows that broadening the focus from the connections between habitat features and selected nests-sites to also include successful sites, multiple scales, and multiple species, will increase our ability to understand a complex system and make sound management decisions.

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Table 2.1: Classification of community types used in the macrohabitat scale models. A total of 15 cover types were classified using literature, digital orthophotos, and field observations. The four most abundant habitat types (shown as '% at nest') found at nests were included in the models, while the remaining community types were categorized as 'other'.

Cover Type	**Model Variable**	**Description**	**% at nest**
Active Dunes	Active_dune	Active building dunes, with plants such as beach elder (*Iva imbricata*), sea oats (*Uniola paniculata*) and beach croton (*Croton punctatus*). Usually primary dune ridge, just behind wrack line. Can be semi-permanent and well developed.	**67.2***
Beach Pond	Other	A permanent or semi-permanent body of water, usually brackish, sometimes tidally influenced and can be connected to the ocean on the front side of the beach, or the marsh on the backside of the beach.	0.0
Dead Wax Myrtle	Other	Areas of extensive dead wax myrtle (*Morella cerifera)*, usually killed due to tidal inundation. Occasionally large shrubs (*Baccharis halimifolia)* may also be present.	0.0
Dense *Spartina patens*	Other	Monoculture areas of *Spartina patens.*	2.9
Fiddler Crab Salt Pan	Other	Open muddy areas with limited vegetation, dominated by fiddler crabs. May be near tidal creeks on back beaches, or near beach ponds. Usually muddy substrates that get washed over on highest tides.	2.1
Inactive dunes	Other	Well-established dunes, vegetated with species such as *Diodia teres, Eupatorium capillifolium*, *Conyza canadensis,* usually at least one or two primary dune ridges west of the ocean.	3.7
Interdune Meadow	Interdune_ meadow	Low, vegetated areas, generally dominated by low growing plants, grasses, and forbs such as *Phyla nodiflora, Sabatia stellaris, Cyperus retrorsus*.	**6.2***
Interdune Swale	Other	Low areas, between dunes, not heavily vegetated, precursor to Interdune meadow.	3.2
Marsh	Other	Marsh, dominated by vegetation such as *Spartina alterniflora, Juncus roemerianus,* intersected by tidal creeks.	0.0
Open beach	Open _beach	Open, non-vegetated sand above the tideline, but not landward of the primary dunes.	**4.4***
Open beach low tide	Other	Open beach below the high tide line.	0.00
Open sand	Other	Open sand landward of the first primary dunes. Non-vegetated.	2.5
Overwash beach	Overwash_ beach	Open beach that is frequently washed over. May be vegetated with high salt tolerant species, such as *Salsola kali*, *Borrichia frutescens*, and *Ipomoea pes-caprae*. Experiences tidal overwash on extreme tide events only. May be scoured by wind or exhibited as overwash fans. Early successional.	**5.5***
Salicornia	Other	Patches of salicornia (*Salicornia virginica*) and sea purslane (*Sesuvium portulacastrum*). More vegetated than fiddler crab salt pans. Often found on back beaches, near inlets, and in areas with some level of tidal inundation. Generally low elevation.	1.9
Wax myrtle	Other	Medium to tall shrubs of both *Morella cerifera* and *Baccharis halimifolia.*	0.3

Table 2.2: Nest site selection models for Wilson's Plovers and American Oystercatchers. The top model is shown along with those models considered competitive (within Δ 2 AIC$_c$ units) which were advanced to the multi-scale model, as well as the null model, for comparison.

Nest Site Selection Models

Microhabitat

Sp.	Model	Dev.	K	ΔAIC$_c$	w_i
WIPL	Site + Year + Nest in Veg + Wrack Cover + Elevation + Open + Shell Cover	909.61	8	0.00	0.51
	Site + Year + Nest in Veg + Wrack Cover + Elevation + Open	913.10	7	1.45	0.24
	Site + Year + Nest in Veg + Wrack Cover + Elevation + Shell Cover	913.48	7	1.82	0.21
	Null (Site + Year)	1192.213	3	272.46	0.00
AMOY	Site + Year + Wrack Cover + Open	134.85	5	0.00	0.23
	Site + Year + Wrack Cover + Open + Nest In Veg	133.19	6	0.57	0.18
	Site + Year + Wrack Cover + Open + Shell Cover	133.93	6	1.30	0.12
	Site + Year + Wrack Cover + Open + Elevation	133.93	6	1.31	0.12
	Null (Site + Year)	160.81	3	21.63	0.00

Macrohabitat

Sp.	Model	Dev.	K	ΔAIC$_c$	w_i
WIPL	Site + Year + Open Beach + Other Community + Dist. To Upland + Dist. To Tideline	2169.45	7	0.00	0.28
	Site + Year + Open Beach + Overwash Beach + Other Community + Dist. To Upland + Dist. To Tideline	2168.27	8	0.78	0.19
	Site + Year + Open Beach + Interdune Meadow + Other Community + Dist. To Upland + Dist. To Tideline	2168.83	8	1.39	0.14
	Site + Year + Open Beach + Active Dunes + Other Community + Dist. To Upland + Dist. To Tideline	2169.34	8	1.90	0.11
	Site + Year + Open Beach + Other Community + Dist. To Marsh + Dist. To Upland + Dist. To Tideline	2169.41	8	1.97	0.10
	Null (Site + Year)	2548.67	3	365.18	0.00
AMOY	Site + Year + Active Dunes + Overwash Beach + Other Community + Dist. To Marsh + Dist. To Upland + Dist. To Tideline	461.08	9	0.00	0.28
	Site + Year + Active Dunes + Overwash Beach + Dist. To Marsh + Dist. To Upland + Dist. To Tideline	463.71	8	0.63	0.21
	Site + Year + Active Dunes + Overwash Beach + Open Beach + Dist. To Marsh + Dist. To Upland + Dist. To Tideline	462.36	9	1.29	0.15
	Site + Year + Open Beach + Interdune Meadow + Other Community + Dist. To Marsh + Dist. To Upland + Dist. To Tideline	462.43	9	1.36	0.14
	Site + Year + Active Dunes + Overwash Beach + Interdune Meadow + Dist. To Marsh + Dist. To Upland + Dist. To Tideline	462.96	9	1.89	0.11
	Site + Year + Active Dunes + Overwash Beach + Interdune Meadow + Other Community + Dist. To Marsh + Dist. To Upland + Dist. To Tideline	461.02	10	1.96	0.11
	Null (Site + Year)	565.91	3	92.78	0.00

Table 2.3: Parameter estimates for nest site selection at the microhabitat scale, shown by species, estimated using the top-ranked model, or model-averaged estimates where multiple models were competitive. Informative parameters (confidence intervals that do not cross zero) are indicated with an asterisk (*).

Microhabitat Nest Selection Model Parameter Estimates				
Sp.	**Parameter**	**Estimate**	**2.5 %CI**	**97.5% CI**
WIPL	(Intercept)	-0.78	-1.12	-0.44
	Wrack Cover*	0.68	0.44	0.92
	Shell Cover	0.15	-0.01	0.32
	Openness*	-0.26	-0.49	-0.02
	Elevation*	0.31	0.13	0.48
	Nest In Veg (Y)*	2.16	1.63	2.71
	Site (LSSI)	0.11	-0.25	0.46
	Year (2013)	-0.28	-0.61	0.04
AMOY	(Intercept)	1.66	0.01	3.46
	Wrack Cover*	0.07	0.03	0.14
	Openness*	-0.02	-0.04	-0.01
	Site (LSSI)	-0.11	-1.00	0.79
	Year (2013)	-0.37	-1.24	0.48

Table 2.4: Parameter estimates for nest site selection at the macrohabitat scale, shown by species, estimated using the top-ranked model, or model-averaged estimates where multiple models were competitive. Informative parameters (confidence intervals that do not cross zero) are indicated with an asterisk (*).

Sp.	Parameter	Estimate	2.5 %CI	97.5% CI
WIPL	(Intercept)	-2.18	0.01	3.46
	Active Dunes	0.03	-0.17	0.23
	Interdune Meadow	0.04	-0.06	0.13
	Overwash Beach	-0.05	-0.15	0.04
	Open beach*	-0.85	-1.05	-0.66
	Other Community*	-0.95	-1.11	-0.79
	Dist. To Upland*	0.40	0.28	0.51
	Dist. To Tideline*	-0.38	-0.51	-0.24
	Dist. To Marsh	-0.01	-0.15	0.12
	Site (LSSI)*	-0.33	-0.58	-0.07
	Year (2013)	-0.03	-0.19	0.25
AMOY	(Intercept)	-5.38	-6.14	-4.63
	Active Dunes*	0.91	0.40	1.43
	Interdune Meadow	-0.07	-0.58	0.44
	Overwash Beach*	0.51	0.25	0.76
	Open beach	-0.17	-1.12	0.78
	Other Community	-0.75	-1.74	0.23
	Dist. To Upland*	0.35	0.08	0.62
	Dist. To Tideline*	-1.01	-1.47	-0.56
	Dist. To Marsh	-0.78	-1.40	-0.17
	Site (LSSI)*	0.21	-0.49	0.91
	Year (2013)	0.42	-0.12	0.97

Table 2.5: Nest survival models for Wilson's Plovers and American Oystercatchers. The top-ranked model is shown along with those models considered competitive (within Δ 2 AIC$_c$ units) which were advanced to the multi-scale model, as well as the null model, for comparison.

Nest Survival Models

Microhabitat					
Sp.	**Model**	**Dev.**	**K**	**ΔAIC_c**	**w_i**
WIPL	Site + Year + Openness + Wrack Cover	1964.18	5	0	0.17
	Site + Year + Openness + Wrack Cover + Nest In Veg	1963.24	6	1.07	0.10
	Site + Year + Openness + Wrack Cover + Elevation	1963.44	6	1.27	0.09
	Site + Year + Openness	1967.96	4	1.76	0.07
	Site + Year + Openness + Wrack Cover + Shell Cover	1963.96	6	1.79	0.07
	Null (Site + Year)	1192.213	3	272.46	0.00
AMOY	Site + Year + Nest In Veg	321.26	4	0.00	0.12
	Null (Site + Year)	323.74	3	0.43	0.09
	Site + Year + Nest In Veg + Shell Cover	321.09	5	1.53	0.05
	Site + Year + Shell Cover	322.57	4	1.55	0.05
	Site + Year + Openness	323.26	4	1.83	0.05
	Site + Year + Nest In Veg + Elevation	321.09	5	1.90	0.05
Macrohabitat					
Sp.	**Model**	**Dev.**	**K**	**ΔAIC_c**	**w_i**
WIPL	Site + Year + Active Dunes + Overwash Beach + Other Community + Dist. To Upland	1914.34	7	0.00	0.23
	Site + Year + Active Dunes + Open Beach + Interdune Meadow + Other Community + Dist. To Upland	1913.41	8	1.09	0.13
	Site + Year + Active Dunes + Open Beach + Overwash Beach + Interdune Meadow + Dist. To Upland	1913.41	8	1.09	0.13
	Site + Year + Open Beach + Overwash Beach + Interdune Meadow + Other Community + Dist. To Upland	1913.41	8	1.09	0.13
	Site + Year + Active Dunes + Overwash Beach + Interdune Meadow + Other Community + Dist. To Upland	1913.41	8	1.09	0.13
	Site + Year + Active Dunes + Open Beach + Overwash Beach + Other Community + Dist. To Upland	1913.41	8	1.09	0.13
	Site + Year + Active Dunes + Overwash Beach + Other Community + Dist. To Marsh + Dist. To Upland	1914.26	8	1.97	0.08
	Null (Site + Year)	1952.27	3	29.88	0.00
AMOY	Site + Year + Dist. To Tideline	321.38	4	0.00	0.12
	Null (Site + Year)	323.74	3	0.32	0.10
	Site + Year +Open Beach + Dist. To Tideline	320.01	5	0.70	0.08
	Site + Year + Dist. To Tideline + Dist. To Upland	320.19	5	0.87	0.08
	Site + Year + Dist. To Upland	322.49	4	1.18	0.07
	Site + Year + Open Beach	322.56	4	1.19	0.07
	Site + Year + Other Community + Dist. To Tideline	321.11	5	1.80	0.05
	Site + Year + Other Community	323.23	4	1.85	0.05

Table 2.6: Parameter estimates for nest survival at the microhabitat scale, shown by species, estimated using the top-ranked model, or model-averaged estimates where multiple models were competitive. Informative parameters (confidence intervals that do not cross zero) are indicated with an asterisk (*).

Sp.	Parameter	Estimate	2.5 %CI	97.5% CI
WIPL	(Intercept)	2.41	1.95	2.87
	Wrack Cover	-0.01	-0.01	0.00
	Shell Cover	-0.01	-0.03	0.02
	Openness*	-0.01	-0.01	-0.00
	Elevation	-0.09	-0.28	0.11
	Nest In Veg (Y)	-0.16	-0.50	0.18
	Site (LSSI)*	0.42	0.17	0.67
	Year (2013)*	0.59	0.35	0.84
AMOY	(Intercept)	1.50	0.40	2.60
	Nest In Veg (Y)	0.76	-0.32	1.85
	Shell Cover	-0.03	-0.09	0.03
	Openness	0.00	-0.02	0.01
	Elevation	0.13	-0.53	0.80
	Site (LSSI)*	1.49	0.79	2.19
	Year (2013)	0.36	-0.32	1.85

Table 2.7: Parameter estimates for nest survival at the macrohabitat scale, shown by species, estimated using the top-ranked model, or model-averaged estimates where multiple models were competitive. Informative parameters (confidence intervals that do not cross zero) are indicated with an asterisk (*).

Sp.	**Parameter**	**Estimate**	**2.5 %CI**	**97.5% CI**
WIPL	(Intercept)	-2.52	0.91	4.12
	Active Dunes	-0.00	-0.02	0.02
	Interdune Meadow	0.01	-0.00	0.03
	Overwash Beach*	-0.02	-0.03	-0.01
	Open beach	0.01	-0.01	0.03
	Other Community	-0.01	-0.02	0.01
	Dist. To Upland*	-0.00	-0.00	-0.00
	Dist. To Marsh	0.00	-0.00	0.00
	Site (LSSI)*	0.50	0.16	0.83
	Year (2013)*	0.72	0.50	0.96
AMOY	(Intercept)	1.69	0.69	2.69
	Open beach	-0.18	-0.51	0.14
	Other Community	-0.09	-0.37	0.20
	Dist. To Upland	0.24	-0.20	0.65
	Dist. To Tideline	0.35	-0.12	0.81
	Site (LSSI)*	1.34	0.31	2.37
	Year (2013)	0.42	-0.25	1.09

Table 2.8: Multi-scale models for nest survival of Wilson's Plover and American Oystercatcher nests. Models were ranked and the top-ranked model or set of competitive models (those that are ranked above the null and do not include uninformative parameters) are shown.

Nest Survival Models					
Scales Combined					
Sp.	**Model**	**Dev.**	**K**	**ΔAIC_c**	**w_i**
WIPL	Site + Year + Active Dune + Overwash Beach + Other Community + Dist. To Upland (Macro Scale)	1914.34	7	0.00	0.23
	Site + Year + Active Dune + Open Beach + Interdune Meadow + Other Community + Dist. To Upland (Macro Scale)	1913.41	8	1.09	0.13
	Null (Site + Year)	1952.26	3	29.88	0.00
AMOY	Site + Year + Nest In Veg (Micro Scale)	321.26	4	0.00	0.09
	Site + Year + Dist. To Tideline (Macro Scale)	321.38	4	0.12	0.09
	Null (Site + Year)	323.74	3	0.43	0.08

Table 2.9: Parameter estimates for nest survival from the best ranked model in the multi-scale comparison shown by species, estimated using the top-ranked model, or model-averaged estimates where multiple models were competitive. Informative parameters (confidence intervals that do not cross zero) are indicated with an asterisk (*).

Sp.	Parameter	Estimate	2.5 %CI	97.5% CI
WIPL	(Intercept)	2.84	2.34	3.39
	Active Dune	0.00	-0.02	0.02
	Overwash Beach*	-0.02	-0.03	-0.01
	Other Community	0.00	-0.02	0.02
	Open Beach*	0.02	0.01	0.03
	Interdune Meadow*	0.02	0.01	0.03
	Dist. To Upland*	-0.001	-0.002	-0.000
	Site (LSSI) *	0.68	0.41	0.96
	Year (2013) *	0.73	0.5	0.97
AMOY	(Intercept)	1.72	0.74	2.69
	Nest In Veg (Y)	0.78	-0.3	1.86
	Dist. To Tideline	0.35	-0.12	0.82
	Site (LSSI)*	1.23	0.31	2.14
	Year (2013)	0.38	-0.29	1.06

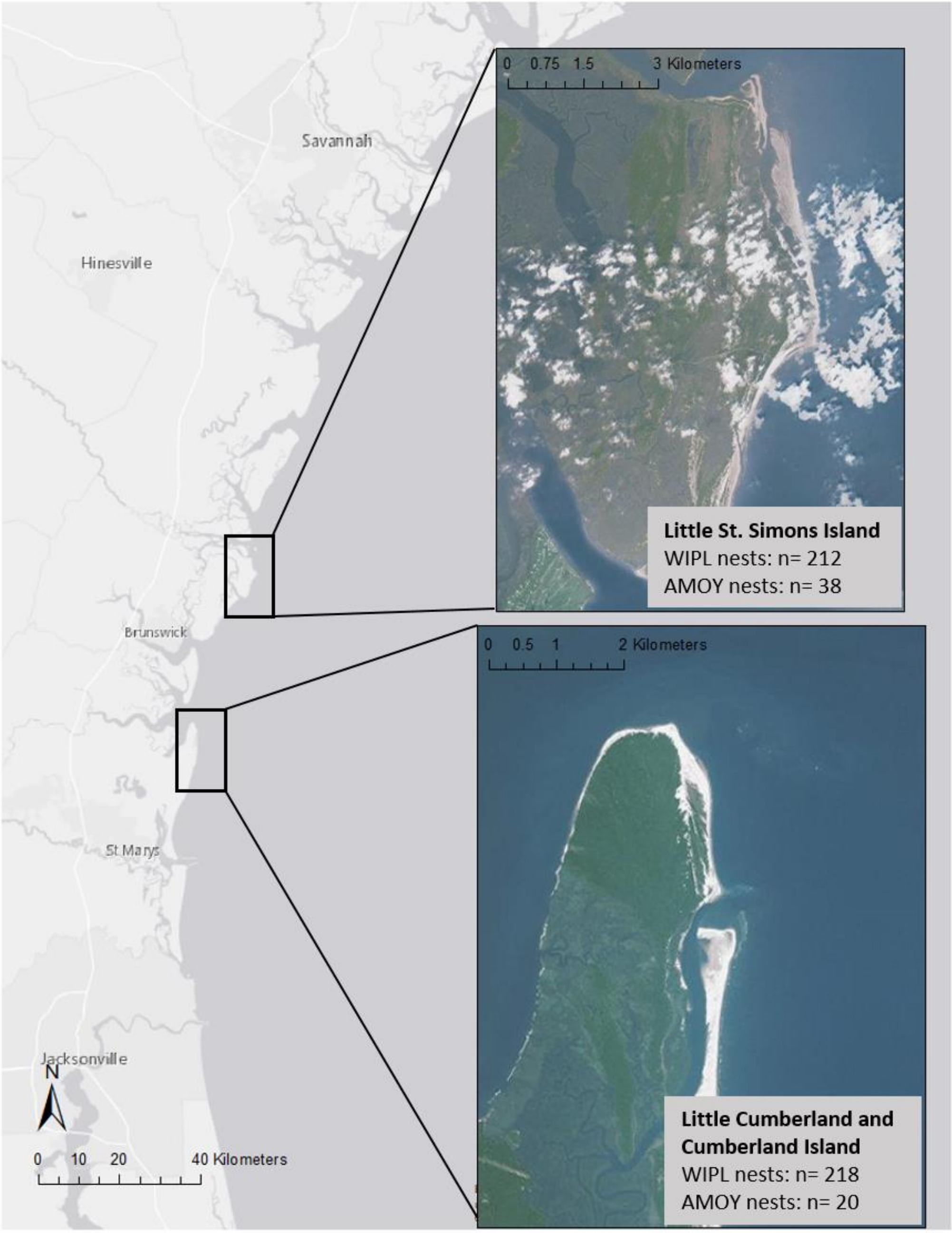

Figure 2.1: Study areas shown in relationship to position along the Georgia coast, with insets of Little St. Simons Island and Little Cumberland and Cumberland Island. Nest numbers are totaled from the 2012 and 2013 field season, and shown inset with imagery of both islands.

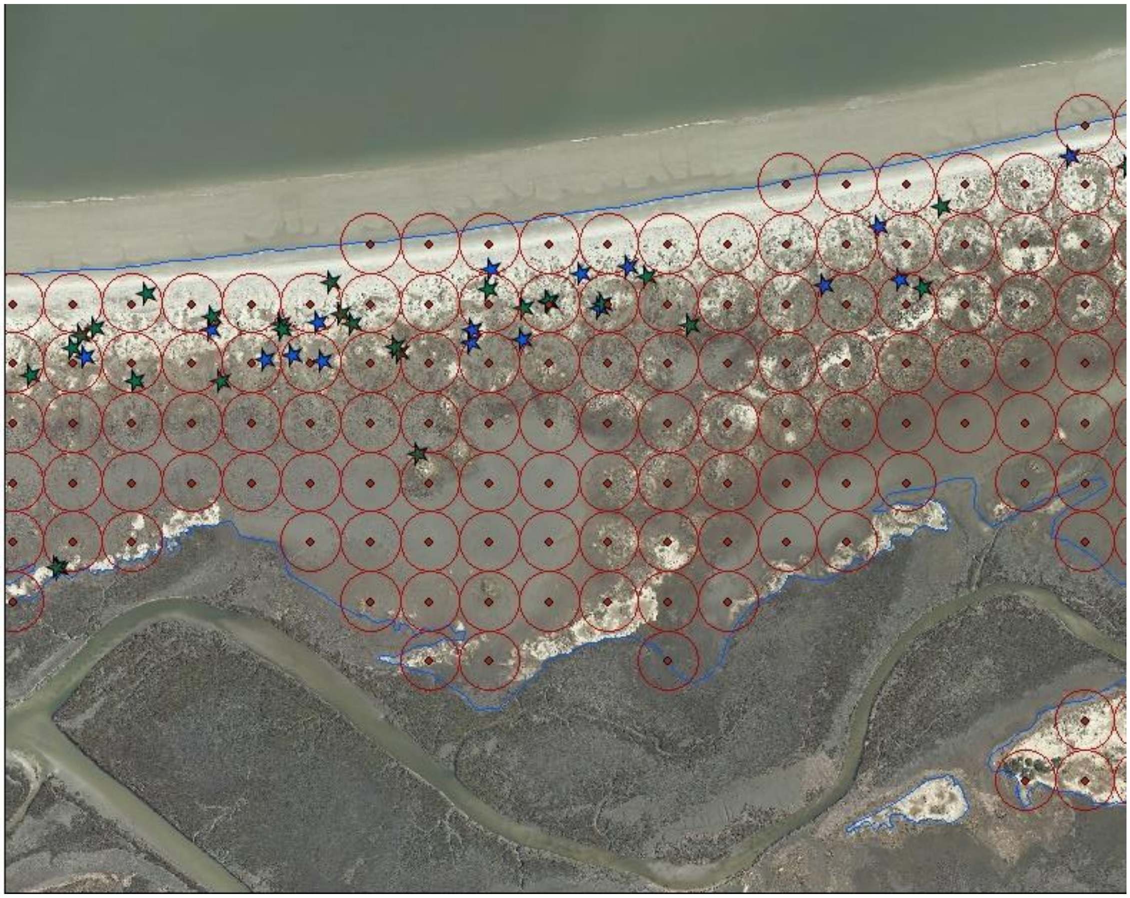

Figure 2.2: Schematic showing nest locations (denoted with green and blue stars) and the systematic array of points (denoted by the red points), as well as the 25-meter radius buffer around each point. Points were located at 50-meter intervals to prevent overlapping buffers, and community composition within each point was sampled to quantify the available habitat.

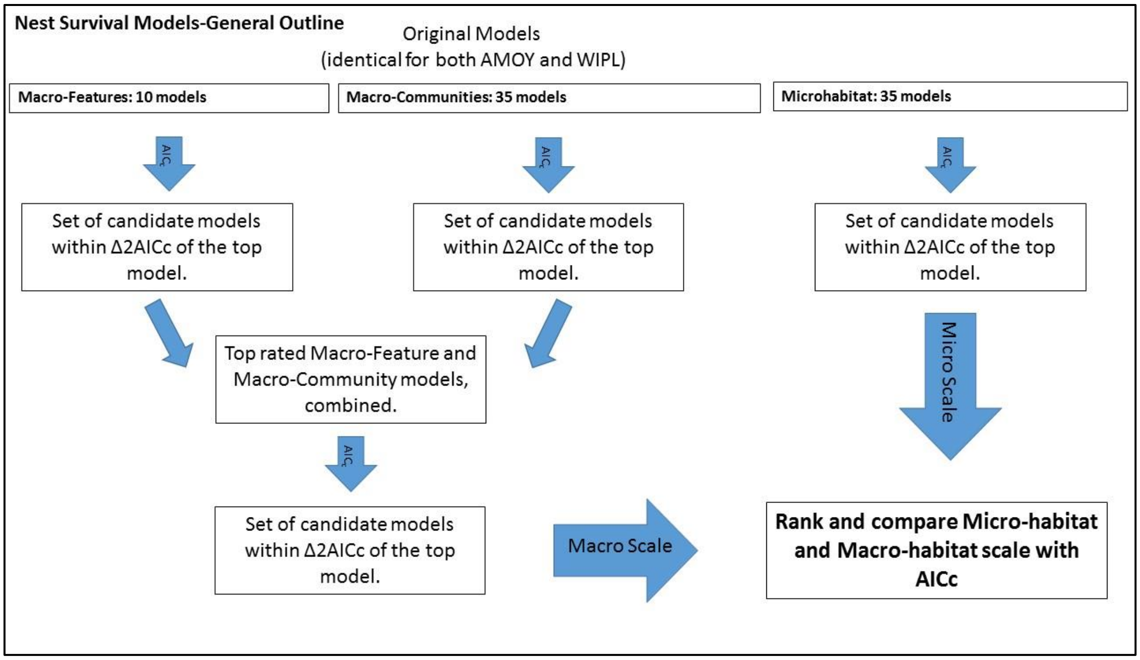

Figure 2.3: Flow chart of the model-selection process for nest survival models for both Wilson's Plovers and American Oystercatchers. Both the microhabitat and the macrohabitat scales were compared directly using AICc to rank models.

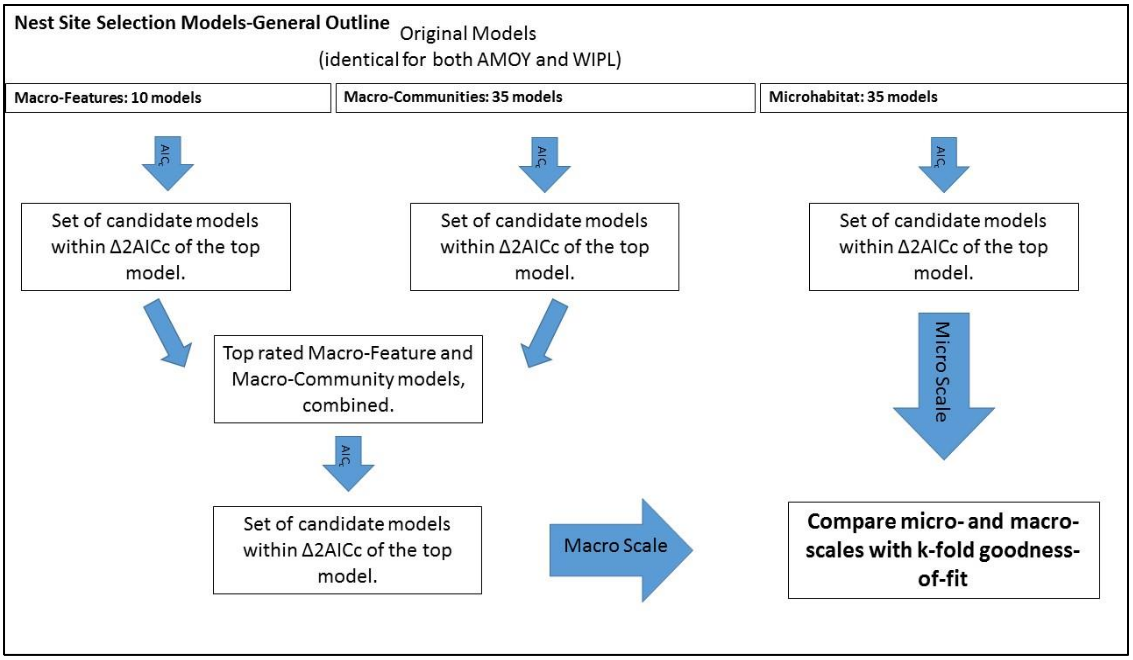

Figure 2.4: Flow chart of the model-selection process for nest site selection models for both Wilson's Plovers and American Oystercatchers. Both the microhabitat and the macrohabitat scales were compared using the *k*-fold goodness of fit score for each scale.

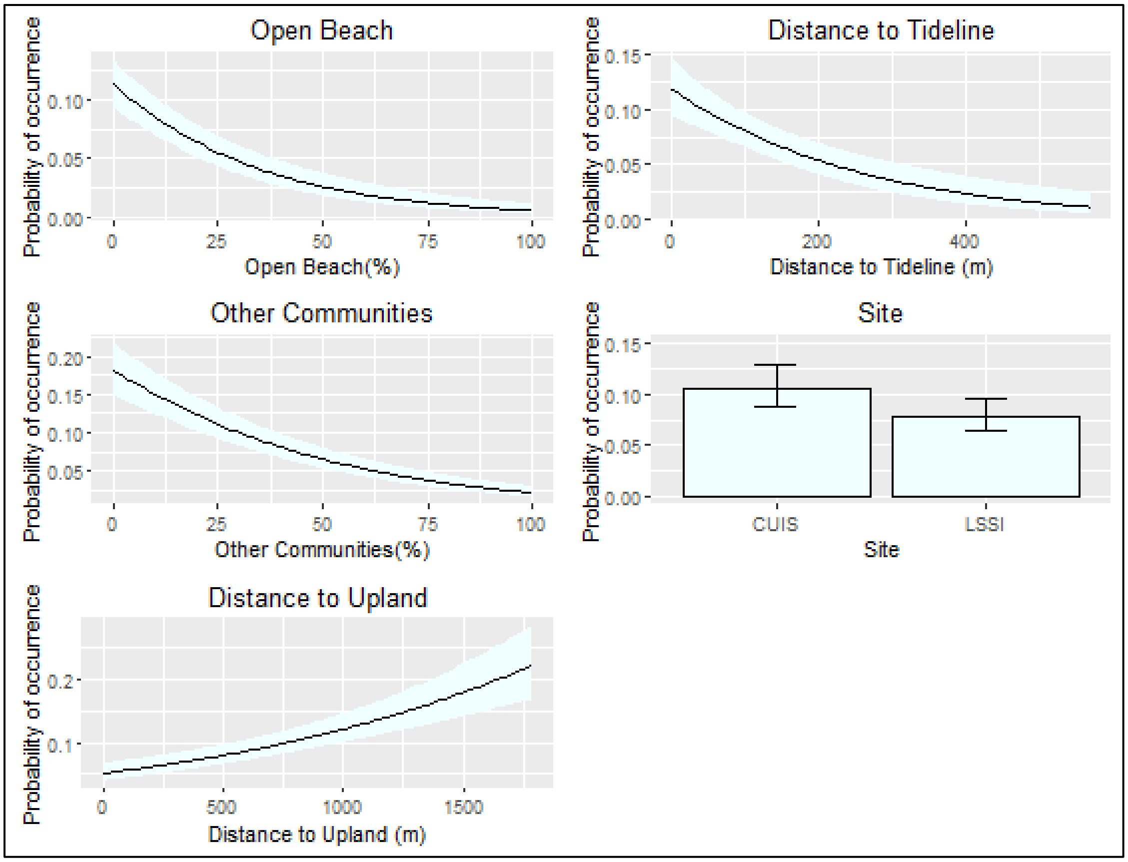

Figure 2.5: Predicted probability of selection of nest sites for Wilson's Plovers based on the top-ranked model from the macrohabitat scale, which was shown to be the most informative scale. Lines are mean predictions and shaded areas are 95% confidence intervals. All habitat features shown had confidence intervals that did not include zero, and are therefore considered informative.

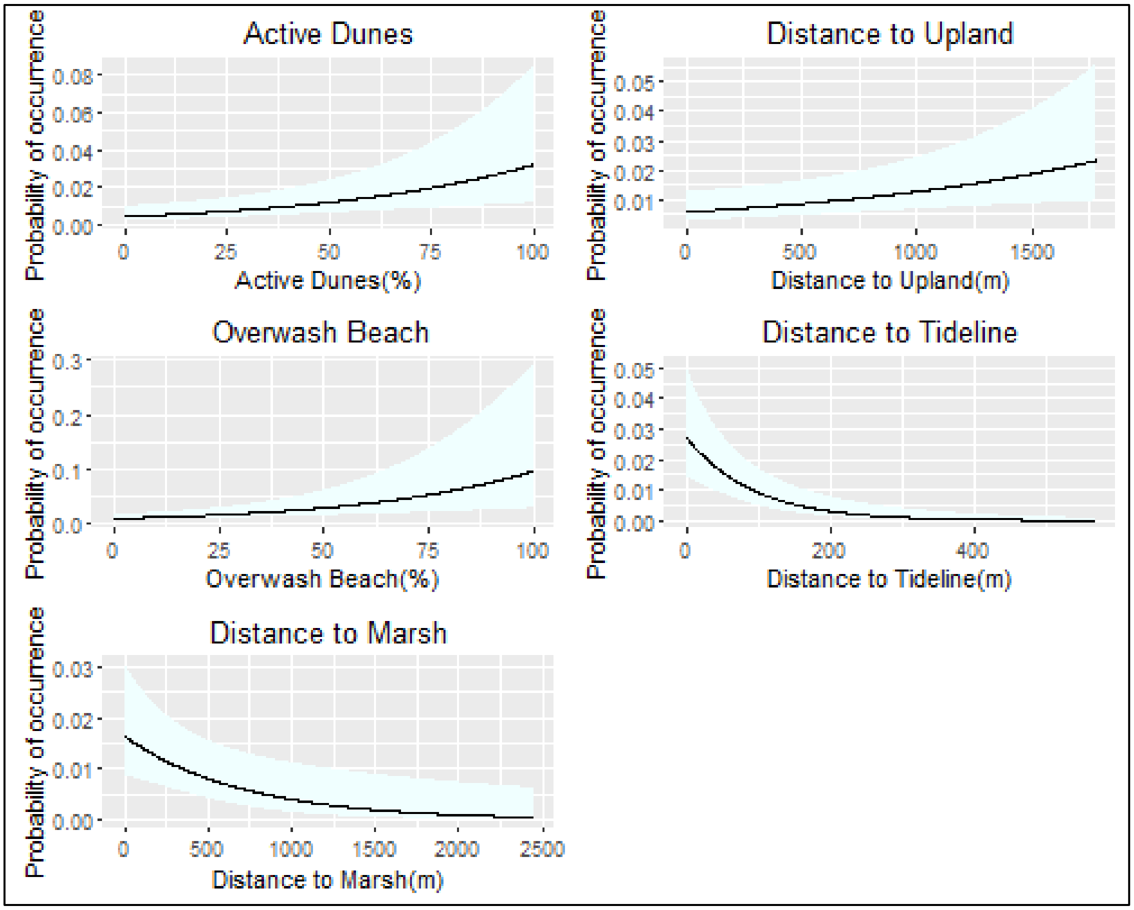

Figure 2.6: Predicted probability of selection of nest sites for American Oystercatchers based on the top model from the macrohabitat scale, which was shown to be the most informative scale. Lines are mean predictions and shaded areas are 95% confidence intervals. All habitat features shown had confidence intervals that did not include zero, and are therefore considered informative.

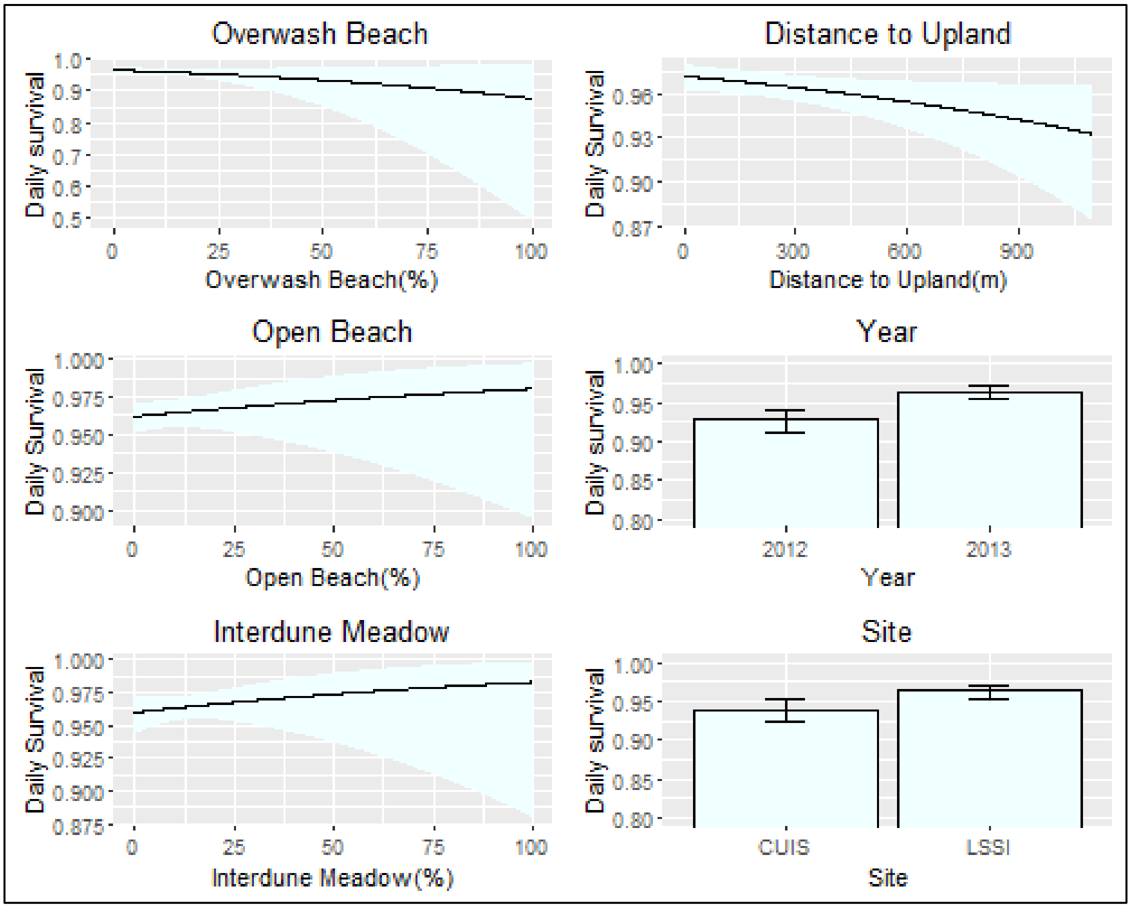

Figure 2.7: Predicted daily survival probability for Wilson's Plover nests based on the top two averaged models from the macrohabitat scale, which ranked best in the multi-scale comparison. Lines are mean predictions and shaded areas are 95% confidence intervals. All habitat features shown had confidence intervals that did not include zero, and are therefore considered informative.

CHAPTER 3

ASSESSING THE COMPETING RISKS OF OVERWASH AND PREDATION OF SHOREBIRD NESTS IN A CHANGING ENVIRONMENT[2]

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[2] Sterling, A. V., T. Keyes, S. D. Coleman, C. W. Jackson, Jr., and R. J. Cooper. To be submitted to *The Auk.*

ABSTRACT

The two main threats to nest success for shorebirds on the Georgia coast are tidal overwash, which results in the subsequent flooding or downing of eggs, and predation. We assessed how predation and overwash influenced nest success of the Wilson's Plover (*Charadrius wilsonia*), a species of conservation concern, and whether we could predict nest outcomes based on habitat features. We used multinomial models to investigate each risk separately while simultaneously estimating the probability of each fate. We incorporated habitat features into these models to determine how emergent threats of a non-native predator and shoreline changes due to sea level rise might impact the success of this species. Nests experienced a higher risk of predation than overwash, but predation was not well predicted using habitat features. We did not distinguish differences in survival risk due solely to a novel predator. While the risk of overwash was influenced by habitat features such as elevation, community type and accretion rates, it was variable by year. Shoreline change rates were not strongly predictive in our models, however we maintain that incorporating data about shoreline dynamics into shorebird management is important for predicting habitat use, and that future research should explore these connections.

INTRODUCTION

Nest success is an important component of reproductive success for birds, and increasing or maintaining high levels of reproductive success is critical for maintaining species of concern (Stahl and Oli 2006, Clark and Martin 2007, Brown 2013, Cunningham et al. 2016). Many studies that have focused on shorebird nesting ecology found that, because site selection is an adaptive behavior, habitat features can be useful indicators of success (Kellner et al. 1992, Misenhelter and Rotenberry 2000). For example, features such as increased vegetation at nests, or cryptic nesting substrate (Burger 1987, Corbat 1990, Pampush and Anthony 1993) can reduce predation risk. Other threats to nest success can include nest parasitism which can be predicted by location of nests in relation to edge habitat (Paton 1994), or proximity to food resources which can be measured by territory quality (Ens et al. 1992). However, some previous work has shown that habitat features may be better at predicting nest site selection rather than success (Chapter 2; Corbat 1990, Wilson and Cooper 1998, Zdravkovic 2010) and usually the associations between habitat choice and risk is speculative (Vanhorne 1983, Chalfoun and Schmidt 2012). Particularly, when Wilson's Plover nests from this dataset were analyzed using binomial models, habitat features were better predictors of nest site selection than they were of nest success (see Chapter 2).

The lack of congruence between habitat features and nest success could be due to multiple forces within a landscape influencing the success or failure of nests (Jones 2001). Additionally, tradeoffs between different causes of nest failure may exist which can further reduce the ability of habitat features to be a good indicator of nest success (Etterson et al. 2007b, Hunter et al. 2016). For example, nesting near vegetated dunes could increase the risk of predation, while nesting farther from dunes and nearer to the tideline might increase the risk of flooding (Burger 1987). Rather than focusing only on two fates, successful versus failed nests, we wanted to understand how different causes of nest failure affect the ability of habitat features to be predictive.

For shorebirds nesting on the Georgia coast, the two main threats to nest success are tidal overwash, which results in the subsequent flooding or downing of eggs, and predation (Corbat and Bergstrom 2000, George 2002). Understanding how predation and overwash influence nest success, and whether we can predict nest outcomes based on habitat features in areas surrounding nests, are important information for conservation and management. Traditionally, the most common way to investigate multiple causes of nest failure was using apparent or observed failure rates; however, these estimates are generally subject to discovery bias which falsely inflates estimates (Mayfield 1975, Etterson et al. 2007a). Using multinomial models to model nest failure allows us to look at each risk separately while estimating the probability of each nest's outcome simultaneously, and by incorporating habitat features we can better understand how the environment influences these risks (Etterson et al. 2007a, Etterson et al. 2007b). This information can be used to highlight how intrinsic and extrinsic factors interact to influence nest success simultaneously (Sherry et al. 2015) or how nest site selection affects tradeoffs when balancing predation risk with other risks (DeRose-Wilson et al. 2013, Hunter et al. 2016). Particularly in highly dynamic environments, like the Georgia coast, rapid changes are occurring in risks that birds face, and a more detailed investigation into the components of nest failure is necessary.

While the risk of tidal overwash can be influenced by spatial habitat characteristics, such as distance to the high tideline, distance to the marsh edge and elevation of the nest, changes to shorelines are also likely influential (Sims et al. 2013). Shoreline change is natural and highly variable in Georgia (Jackson 2015), but rates and locations of change are influenced by sea level rise and inlet dynamics as well, which could influence shorebird nest success and overall productivity (van de Pol et al. 2010a, Aiello-Lammens et al. 2011, Linhoss et al. 2013, Sims et al. 2013). Although many ocean-facing barrier island beaches on the Georgia coast have experienced a net growth, or accretion since the mid 1800's, there are some regions that have an overall trend of erosion (Jackson 2010). Furthermore, some areas with long term accretion trends have experienced substantial erosion since the 1970s (Jackson 2010). Accretion potentially could create nesting habitat for birds; as sand is deposited seaward on regressive Georgia islands (Jackson 2010), vegetation eventually colonizes and stabilizes beaches. Many species of shorebirds prefer nesting in areas of high accretion, where habitat may be overwashed on extreme tides and vegetation remains low in density (Cohen et al. 2009, Erwin et al. 2011, Nol and Humphrey 2012).

Erosion, on the other hand, can result in a loss of nesting or feeding habitat, and has been shown to influence habitat use by shorebirds (Revell et al. 2011, Walter et al. 2013). Where net erosion is occurring, it is usually most pronounced along upland and sandy areas on barrier island beaches (Jackson 2015). Additionally, effects of climate change such as rising sea level and increased intensity and duration of storms are predicted to increase rates of erosion and risk of tidal overwash for nests (Rounds et al. 2004, Sims et al. 2013). The risk for tidal overwash could also be influenced by the both the stability of the shoreline and how much movement there is of a shoreline over time. Some regions of a shoreline are highly dynamic and variable, especially near inlets, and could see greater rates of erosion (Jackson 2015). The size of inlets, as well as features such as water flow and historic channelization, can greatly influence inlet stability (Jackson et al. 2006). Inlets are important areas for beach nesting birds, providing both nesting and foraging sites (Cohen et al. 2009, DeRose-Wilson et al. 2013, Zdravkovic 2013), so understanding how these areas influence overwash risk is important.

An additional component of nest failure that is of particular interest on the Georgia coast is predation. For nests at our study sites predation appears to be the dominant cause of nest failure, therefore understanding how habitat features might be predictive specifically of predation could be very useful for management. Numerous studies have considered predation risk to be important, and show that changes in assemblages of predators can have a pronounced impact on nesting shorebirds (Hackney et al. 2013). Species that benefit from human dominated landscapes, such as raccoons (*Procyon lotor*), Fish Crows (*Corvus ossifragus*) and gulls (Family Laridae) have become increasingly common in some regions (Garrott et al. 1993, Martin et al. 2010). Additionally, non-native predators are a serious concern as well; on the Georgia barrier islands coyotes (*Canis latrans*) have expanded their range and have become a significant threat to nesting shorebirds. The impacts of coyotes are thought to be site specific, and can be especially pronounced in small or isolated geographic areas where seasonally available food resources are abundant (Hackney et al. 2013). By investigating the risk of predation independently of other causes of nest failure, we can determine if either risk or habitat choice is changing in response to the novel threat of coyotes.

To investigate how these emergent threats might influence nest success of shorebirds on the Georgia coast, we focused our research on the Wilson's Plover (*Charadrius wilsonia*). Due to habitat loss and human disturbance, the range of this species is contracting (Zdravkovic 2013) and in response, it has been designated as a high regional conservation priority by the US Shorebird Conservation Plan and within the Atlantic Flyway (Brown 2001, Brown 2013). Within Georgia it is listed as threatened (GADNR 2015). Wilson's Plovers nest on the open beaches of barrier islands, and nest sites in Georgia have been characterized as highly variable in terms of the amount of vegetation, wrack and distance to the tideline (Corbat 1990). Several studies have focused on site selection and overall success for this species (Bergstrom 1988, Corbat 1990, Zdravkovic 2010, Ray 2011, DeRose-Wilson et al. 2013), but none have investigated how specific causes of failure influence reproductive success, and more importantly, how habitat features influence specific risks.

Our broad goal was to determine how habitat variables influenced the risks of failure for nests, and also how new emerging threats influenced risk. We predicted that (1) risk of overwash would be affected by elevation and proximity to water, and (2) shoreline change rates would be influential in predicting overwash. Specifically, we predicted that overwash risk would be positively associated with current and historic rates of erosion, and that areas that were more dynamic, such as near inlets, would be at greater risk for tidal overwash. Additionally, we predicted that (3) predation risk would be increased for nests that were not concealed in vegetation, and for nests nearer to predator sources, and (4) there would be significant differences in predation rates or predictive habitat variables at one of our study sites in 2015 compared to the 2012 and 2013 seasons, in response to novel predation pressure due to the establishment of non-native coyotes there.

METHODS

Study Sites

During the 2012, 2013, and 2015 breeding seasons, from mid-March until late July, we monitored two sites that were composed of three barrier islands in coastal Georgia with previously known populations of breeding Wilson’s Plovers (Figure 3.1; Corbat 1990, George and Schweitzer 2004, Sabine et al. 2006). Little St. Simons Island (LSSI; ca. 31.26°N, 81.27°W; 5,260 ha) is a privately owned, undeveloped barrier island located in Glynn County at the southern branch of the Altamaha River Delta. It has approximately 11 km of wide, ocean-front beach with areas of tidal over-wash, preliminary and well-developed dunes with moderate vegetation, and areas of marsh ponds. There are two tidal creeks that bisect the beach to the Atlantic Ocean, and areas of marsh and mudflats that are accessible from the beach front. Cumberland Island (CUIS; 30.85°N, 81.43°W; 14,736 ha), which is designated as a National Seashore, has approximately 29 km of beach, however we focused our efforts on the 4 km stretch of northern beach known as Long Point. Included in this site is Little Cumberland Island (LCI; 30.97°N, 81.41°W; 2,300 ha), which is privately owned and separated from the larger island by a tidal creek. Both LSSI and CUIS serve as important nesting areas for shorebirds, sea birds and sea turtles (Schneider et al. et al. 2010). Heterogeneous plant communities, including active primary dunes dominated by sea oats (*Uniola paniculata*) and beach elder (*Iva imbricata*) and overwash areas dominated by railroad vine (*Ipomoea pescaprae*) and sea purslane (*Sesuvium portulacastrum*) generally compose the vegetation at both sites (Duncan 1982, Schoettle 1984). The backdune areas at these sites range from dense areas of *Spartina patens*, mud flats dominated by *Salicornia spp.*, and marsh dominated by *Spartina alterniflora*. Additionally, the habitat at these sites is a dynamic with areas of both significant erosion and accretion, a tidal amplitude of nearly 3 meters (Figure 3.2), and both sites are considered regressive barrier islands (Davis 2004, Jackson 2010).

Nest Searching and Monitoring

Both sites were divided into thirds where we searched each section every third day to ensure adequate and even coverage and reduced disturbance. Nests were located through behavioral observations of adults, following tracks, and through systematic searches of all available nesting habitat (Powell 2001). Once found, nest locations were recorded using handheld Garmin GPSMAP 60CSx handheld units and monitored every three days throughout incubation. Every effort was made to minimize disturbance. Searching and monitoring were carried out in each section of beach once every three days unless temperatures exceeded 38°C, winds exceeded 20 mph, or if heavy rain was falling. If a beach section was missed on the scheduled day due to weather, monitoring resumed as soon as conditions permitted. If a Wilson's Plover nest was found after clutch completion (three eggs in a nest, or two checks of only one or two eggs), eggs were floated to determine their approximate lay date to aid in banding of chicks for a different study (see Chapter 2; Hood 2006).

A fate was assigned as either successful, when at least one egg hatched, predated, or overwashed. When a nest failed, we determined cause of failure by observing evidence at the nest site. Nests were categorized as predated when tracks of mammalian or avian predators, egg shell or debris, or drag marks leading to ghost crab burrows were present. When clear tracks were visible, we recorded the likely predator, however if eggs were missing and the nest scrape was not flooded, we recorded the nest as predated, with the predator unknown. The nest was recorded as overwashed if the sand was wet, eggs were washed out of the nest cup, or if the high tideline went above the nest. Nests with unknown outcomes, abandoned nests, and nests with non-viable eggs were censored from this study.

Habitat Variables

Once nests were no longer active, a marked wooden dowel was placed in center of the nest cup to mark the elevation. At the conclusion of the nesting season, we measured the elevations of all nests referenced to the marked elevation, using Real Time Kinematic (RTK) satellite navigations GPS (Trimble5800, Trimble Navigation Limited, Sunnyvale, CA; +/-1-2cm accuracy). Nest elevation is an important characteristic that could affect flooding probability (Corbat 1990, Rodrigues 1994, Anteau et al. 2012). We also recorded if the nest cup was located within the vegetation (if more than 50% of the nest cup was surrounded by vegetation). Vegetation at the nest may influence overall success as it could provide cover, act as a windbreak, or may limit the ability of incubating adults to detect predators (Bergstrom 1988, Corbat 1990, Hood 2006, Brown and Brindock 2011, Ray 2011, Nol and Humphrey 2012).

We also categorized the community type that the nest was located in, using field observations, and a fine-scale map of the study sites, hand digitized from a 2012–2013 Coastal GA DMC 4-Band 6-inch 8 Bit Image, zoomed to a map scale between 1:300 and 1:500 resolution to categorize the landscape into distinct communities (Geiss 2010). Communities were differentiated based on the literature and knowledge of the sites and included geomorphic features and the presence of distinct plant species to distinguish unique communities (Duncan 1982, Schoettle 1984). This approach resulted in a total of 10 unique cover types (Table 3.1), which were ground-truthed using 100 points randomly distributed across the study site and were verified as 82% accurately classified.

Using the same imagery (from 2012, 2013 and 2015), we measured distance from each nest location to several habitat features that were digitized at a map scale of 1:500

including tide line, marsh edge, and edge of upland areas using the Euclidean Distance tool in ArcGIS (ESRI 2011). Features were digitized in accordance with established protocols implemented by the North Carolina Division of Coastal Management (Geiss 2010). We expected the proximity to these features to influence nest survival, in terms of both predation and overwash risk. For example, edge effects in forests and grasslands have been shown to increase predation risk to nests and these effects may apply to beach nesting birds as well (Paton 1994). Upland areas may provide a source of predators, which could affect nest site selection and daily survival of nests (Lima 2009, Pruner 2010), while distance to tideline and marsh edge might influence flooding risk.

We also quantified shoreline change rates at two different time scales to include as covariates in our models using the AMBUR package (Jackson 2016) in program R (R Development Core Team 2015). The historical dataset included digitized shorelines from 1800-2006 and provided rates for long-term trends, while the current dataset included digitized shorelines from 2007-2015 and assessed short-term changes. Both datasets were created using the same methodologies; first, shorelines were digitized at the high-water line using the wet-dry interface (Camfield and Morang 1996, Jackson 2010) for every time period, then transects were cast perpendicular to those shorelines, and finally intersection points were generated (Jackson et al. 2012). For this analysis, transects were spaced at 50-meter intervals, and then the orientations of the transects were smoothed with a window size of 5 meters using the ‘ambur.filtertran’ function. Intersection points where each transect crossed the shoreline recorded the location of each shoreline over time (Figure 3.3). These intersection, or capture points, were then used for statistical analyses. For the current dataset, we calculated erosion rates (m/yr) using the end-point rate (EPR) method (Jackson et al. 2012) and used the standard deviation of the EPR to quantify temporal variation of the shoreline. The historic shoreline dataset was analyzed using AMBUR-HVA (Jackson 2015), which uses shoreline change rates from AMBUR analyses, in combination with other data to assess risk and coastal hazards (Jackson 2015). From this dataset, we used the shoreline change rate (SCR; m/yr) to quantify erosion and accretion, as well as the standard deviation of the SCR to quantify temporal variation in the shoreline.

Analytical Methods

We modeled the effect of habitat features on the probability of the success, overwash, or predation of our monitored Wilson's Plover nests. We used multinomial models, which allow for multiple fates to be treated as competing risks so that the probabilities of the unique fates are estimated simultaneously (Etterson et al. 2007a). We used MCEstimate (Environmental Protection Agency Midcontinent Ecology Division, Duluth, USA) for this analysis, which is a program designed to use Markov chain algorithms to estimate the probability of each nest outcome, while incorporating nest specific covariates, using maximum likelihood estimates (Etterson et al. 2007b). All covariates were standardized to improve convergence. We combined sites, but analyzed years separately because we were interested in assessing inter-annual variation.

We created a total of 34 additive models including an intercept only model, where each model had two components: overwashed and predated. Habitat variables were combined to influence each component based on our *a priori* hypotheses (Table 3.2). The categorical covariate of community and the continuous covariates of elevation, distance to marsh, distance to tideline, distance to upland as well as the SCR and the standard deviation of the SCR for both the historic and the current time periods were included in the overwash component of the models. We included the categorical covariates of nest located in vegetation (yes or no) and community type, and the continuous covariates of distance to marsh, distance to tideline, and distance to upland in the predation component of the model. Site was included in all models. Each model was created to include environmental covariates for one component at a time, so that when the overwash component included variables, the predation component was set to a null model, with no covariates and vis-versa. We ranked the models using Akaike's Information Criterion corrected for small sample size (AIC_c) to determine which fate was best predicted by habitat features. If habitat features were informative for overwash or predation models individually, and both fell within $\Delta 2$ AIC_c units of the top models, we combined variables from both components into a final set of models and re-ranked them. We used the top model or the top set of models that did not include uninformative parameters (Arnold 2010) to predict daily and period probabilities for each fate, and assessed the effect of all habitat features from those models. For this analysis we based nest-period probabilities on a 25-day incubation period (Zdravkovic 2013). We also assessed goodness-of-fit for the top models using the Hosmer-Lemeshow test (Hosmer and Lemeshow 2000) where we specified 10 groups, and p-values lacking significance ($p > 0.05$) indicated model-fit. Unless otherwise stated, our estimates are reported as means +/- standard errors (SE).

RESULTS

We found a total of 347 nests (2012: 115 located; 2013: 94 located; 2015: 132 located) on CUIS and 377 nests (2012: 97 located; 2013: 115 located; 2015: 165 located) on LSSI. We censored nests with unknown fates, as well as nests with non-viable eggs and abandoned nests to minimize issues associated with classification error, which resulted in including 684 nests in this analysis (Etterson et al. 2007b, Etterson and Stanley 2008). We checked nests every 2.74 (+/- 1.32 [SD]) days, from March 23 when the earliest nest was found, until July 23 when nest monitoring concluded. Our effective sample sizes were: 1,740 in 2012; 2,514 in 2013; and 4,662 in 2015.

During this study, 54.8% of the nests we monitored were predated while 8.6% of the nests were overwashed, which gave us an apparent nest success rate of 36.8%. The primary predator was the coyote, although it should be noted that there was no coyote predation observed on LSSI during the 2012 and 2013 nesting season, and during these years raccoons were the dominant mammalian predator. Avian predation was also substantial, however the dominant category was unknown predator (Figure 3.4), which occurred when there was insufficient evidence to determine the specific predator. There was a considerable amount of variation among years for the number of nests that failed due to tidal overwash (Figure 3.5), with the greatest amount of tidal overwash occurring in 2012.

The mean nest elevation was 2.05 ± 0.03 meters above sea level, and 69% of the nests that we found were located in vegetation. The majority of the nests (63.2%) were located in the active dune community, which is comprised of regions of dune formation just behind the wrack lines, usually vegetated by sea oats, beach elder, and beach croton. Nests at both sites were located, on average, closer to the tideline (81.76 ± 1.75 m) than either the marsh edge (410.14 ± 19.82 m) or the upland edge (497.80 ± 12.61 m). Nest locations had a mean current accretion rate of 10.87 ± 0.68 m/year, and a mean historic accretion rate of 2.61 ± 0.12 m/year. The shoreline is highly dynamic at our study sites;

the average standard deviation of shoreline for the current time period at our nest locations was 29.82 ± 0.96 m/year, and even higher for the historic data set (61.53 ± 21.58 m/year). The shoreline analysis showed that some areas of the ocean facing beach that had historic (1800-2006) rates of accretion experienced erosion during the current (2007-2015) time period (Figure 3.6).

For all three years, the predation component of the models that ranked within Δ 2 AIC_c units of the top model were null models, while the overwash component contained habitat features (Table 3.3). Habitat features that were ranked highly as predictive of overwash varied by year (Table 3.4). In all models, the risk of predation was greater than either the risk of failure due to tidal overwash, or the probability of nest success.

In 2012, our top ranked model included site and elevation, where higher elevation had a negative effect on the probability of a nest failing due to overwash ($\beta = -2.50 \pm 0.94$, Figure 3.7). This model had a weight of 46% and using the Hosmer-Lemeshow test, did not show a lack of fit to the logistic distribution ($p=0.53$). The next best model contained elevation and site along with distance to upland which is considered an uninformative parameter (Arnold 2010).

In 2013, the top model included the community type and elevation as habitat features that influenced the probability of overwash. While elevation did have a negative effect on the probability of overwash ($\beta = -1.39 \pm 1.18$), the 95% confidence interval included zero. In 2013, nests were located in 8 different community types, and only two had an influence on probability of overwash (Figure 3.8). Nests located in overwash beach ($\beta = 2.74 \pm 0.90$) and dense *Spartina patens* ($\beta = 1.98 \pm 0.90$) communities had an increased risk of nest failure due to overwash. The top model had a weight of 53%, and does not show lack of fit (p = 0.07). The next best model had one additional parameter which was distance to the marsh edge, however because it did not improve fit more that $\Delta 2$ AIC_c units, the additional parameter was considered uninformative.

When we ranked the models for the 2015 season, the shoreline change variables were most influential for predicting overwash. Five models were ranked within $\Delta 2$ AIC_c units from the top model, and none of these models had overwhelming support (Table 3.3). The top model included the variable of current shoreline change rate and site, while the second best model included the standard deviation of the current shoreline change rate, and the third best model combined both. Together, these three models made up 36% of the weight, and none exhibited lack of fit (p=0.11, p=0.19, and p=0.09, respectively). From this set of models, current shoreline change rate in the best-ranked model is the only covariate that had an influence on the probability of nest overwash (confidence interval did not contain zero). Despite this variable being informative, the effect, while positive, was very small ($\beta = 0.05 \pm 0.03$, Figure 3.9). Overall survival decreased, and probability of overwash increased with increased shoreline change rates.

Success varied by year, but did not vary significantly by site (Figure 3.10). Survival for the incubation period (25 days) was lowest in 2012 on LSSI (0.11 ± 0.03), and highest in 2015 for both sites (0.47 ± 0.03). The probability of predation ranged from a low 0.52 ± 0.03 at both sites to a high of 0.75 ± 0.03 on CUIS in 2012. Overwash rates were highest in 2012, where nests on CUIS had a probability of 0.22 ± 0.07 and nests on LSSI had a probability of 0.09 ± 0.02 of failing due to tidal overwash. The lowest rates of tidal overwash occurred in 2015 for both sites, where the risk of overwash was essentially zero.

DISCUSSION

Our results revealed that we can distinguish differences between two competing risks to better understand the factors that influence nest survival for Wilson's Plovers. We observed that nests experienced a higher risk of predation than overwash, but contrary to our first hypothesis, predation was not well predicted using habitat features. We also hypothesized that we would see differences in the rate of predation between years without coyote predation and years with coyote predation on LSSI, but this was not reflected in our results. The risk of overwash was influenced by habitat features, which we predicted, however, this risk was variable by year, and different habitat features were predictive in different years. Our second hypothesis addressed the influence of shoreline change rates on overwash risk, but this variable had only a small effect in one year when overwash risk was low. However, future research should continue to explore connections between shoreline dynamics and shorebird habitat, as there may be value for predicting future risks and habitat use (Sims et al. 2013, Jackson 2015).

When multiple threats exist in an environment, it is important to understand how these risks interact simultaneously. Other studies that have used competing risk models highlight that site selection can pose tradeoffs between risks (Hunter et al. 2016). However, we did not find any habitat variables that increased predation risk, so in this case, we cannot draw conclusions about tradeoffs although they likely exist. Regardless of the lack of predictable habitat features influencing predation risk, it is a leading cause of failure on the Georgia coast, as well as in other studies that focus on shorebird productivity (Neuman et al. 2004, Cohen et al. 2009, Collins et al. 2016). In our study the risk of predation is consistently high across years and sites, and when predation risk is high, and risk of overwash is also increased, as we saw in 2012, we observed very low success rates. This could indicate that birds can be moderately successful with high rates of either predation or overwash, but not both. Importantly, during 2012 the success rate that we predicted was low compared to other reported rates for Wilson's Plover, which vary: 25-54% in Texas (Bergstrom 1988), 50-76% in Louisiana (Zdravkovic 2010), 35-45% in North Carolina (Ray 2011, DeRose-Wilson et al. 2013) and 11-55% in a previous study in Georgia (Corbat 1990). Rates of success in Georgia may be comparatively low because of the large tidal amplitude and abundant predators (George 2002), which could act in concert to significantly reduce nest success, as we saw with our results.

Despite its influence on overall nest success, predation was not well predicted by the habitat variables that we incorporated into our models. A subset of these data were analyzed previously using binomial logistic exposure models to investigate how habitat features predicted nest success or failure, and those results showed small effects overall of habitat features on nest success (see Chapter 2). This lack of predictive ability for habitat features in the previous modeling effort may have been largely driven by the predation risk component. It could be possible that other variables that we did not include in our models are better predictors of predation risk, such as abundance, distribution, or type of predators that are present (Lima 2009, Sherry et al. 2015). While this analysis did not reveal strong habitat-influenced patterns predictive of predation risk, strategies are employed by predators that might be predictable. Behavioral foraging strategies of predators, such as using dense clumps of vegetation, dunelets (personal observation), or objects (Page et al. 1985) on the beach as cues to locate nests have been noted. These patterns would not be captured with models that look only at habitat features because they are dependent on behavior as well as the environment surrounding a nest. Additionally, because foraging strategies are a learned behavior (Hackney et al. 2013, Parsons et al. 2013), expanding the focus from only nesting habitat to predator behavior and individual search strategies that are employed would be informative. The risk of predation is not random, it is just not predictable using the habitat features that we included in our models (Wilson and Cooper 1998, Schmidt and Whelan 1999), however it does significantly impact nest success.

The emergent threat of a novel predator is also a serious concern for the overall reproductive success of nesting shorebirds, however, our data do not provide enough detail to investigate how changing predator assemblages influenced risk. We were not able to accurately identify predators at enough nests (30.1 % of predated nests had unknown predators), which makes assessing the direct effect of the predation pressure by non-native coyotes at our sites difficult. We did not see different probabilities of predation between the years when coyote predation was occurring and the years without coyote predation on LSSI. Prior to coyotes becoming the dominant predator, raccoons were the primary mammalian nest predator on LSSI, and have been documented as a significant source of nest failure (Parsons et al. 2013). There are several possible explanations for the lack of difference between predation rates pre- and post-establishment of coyotes. First, both raccoons and coyotes are generalists, with similar search strategies dependent largely on visual and olfactory cues (Parsons et al. 2013, Cherry et al. 2016) . Additionally, interactions between coyote and raccoon may offset predation pressure because coyotes reduce raccoon abundance, either directly or indirectly (Sovada et al. 1995, Rogers and Caro 1998). Therefore, it is difficult to assess if coyotes actually pose an increased risk as a predator, as the predation rates did not differ significantly between the earlier years and the final year of our study. Although a study in Texas documented that coyotes are more likely than raccoons to encounter nests of Northern Bobwhite (*Colinus virginianus*) due to greater nightly travel distances (Cooper et al. 2015), and coyotes are well documented to depredate Wilson's Plover nests and chicks, the risks of coyotes as non-native predators to shorebirds should be documented explicitly.

Overwash risk was low but predictable, however the features predicting overwash varied by year. Previous studies have shown that Wilson's Plovers may be more resilient to overwash than other beach-nesting shorebirds because they tend to nest higher and farther from the tideline than species such as American Oystercatchers and colonial nesting species including Black Skimmers (*Rhychops niger*) and terns (Corbat 1990). Indeed, elevation was an important habitat variable in predicting nest failure in 2012 and 2013, and our results showed that as elevation increased, risk of tidal overwash decreased. Community type was important in predicting the risk of overwash as well. Both the *Spartina patens* and the overwash communities saw an increased risk of overwash. However, these are both community types that are typical of low elevation areas, therefore community type might be confounded with elevation. Shoreline change rate (SCR) in 2015 was the habitat predictor in the top-ranked model; we saw that survival decreased with accretion while overwash risk increased. The effect size was small, but the confidence interval did not include zero. Despite the slight increased risk of overwash, and the corresponding decreased survival, birds may be actively choosing to nest in these accretional areas because they confer some advantage other than nest success (DeRose-Wilson et al. 2013). By avoiding areas of erosion, accretional sites may be appealing because they are building seaward, they usually have low, sparse vegetation, and could provide ample food resources (Erwin et al. 2011). The small effect size and the limited support this model received despite the high ranking is likely due to very few nest failures due to tidal overwash, with only 0.007% of nests influenced by overwash in 2015.

Although overwash risk was not a significant risk in the last year of our study, and we did not see strong effects due to shoreline change rates, we believe that integrating shoreline dynamics with the study of shorebird habitat is a valuable avenue for future research (Sims et al. 2013). It has been projected that even a one centimeter increase in sea level could result in a horizontal shift of up to 1-meter on ocean-facing sandy beaches (Camfield and Morang 1996), however detailed shoreline analysis would be necessary as site-specific variation would influence these rates significantly (Jackson 2010). The local tidal gauge at Fort Pulaski, GA (NOAA tide gauge 8670870) has recorded rising mean sea levels from 1935 -2005 at a rate of 2.98 mm/year (+/- 0.33 mm/yr), which indicates that nesting habitat could be affected (Jackson 2010). For example, shoreline analysis can assist in identifying areas of high risk and vulnerability, especially in light of sea level rise due to climate change (Sims et al. 2013). Programs like AMBUR can identify erosional hotspots, predict how inlets change over time, identify areas of accretion, and reveal overall trends (Jackson 2015), all of which have implications for not only nesting habitat, but also for predicting roosting and foraging locations. There are also morphological features on the landscape that might be useful for predicting areas of high risk, such as overwash fans. These areas can be identified by the presence of visible shoals, or outcrops of mud that result in rapid landward growth of the beach as sand is pushed back with tidal overwash (Deery and Howard 1977). Overwash fans are visible in aerial images, and their presence and components could easily be included in future models to assess their influence on overwash risk.

Understanding the influence and predictability of risks can highlight successful strategies for managers. Predator management is a tool that has been long employed and is critical to the success of not just nests but chick survival as well (Pauliny et al. 2008, Martin et al. 2010), even though predation risk is not identifiable using habitat features for cues. The results from this study showed that predation risk was consistently high, however we saw that the risk of predation was highest when overwash risk was also high, and during these times, nest success was significantly lower. Therefore we recommend that predator management should be increased during times of high overwash risk, whether that overwash risk is a result of sea level rise, shoreline change or in areas of low elevation habitat to reduce pressure on nesting success. Another possible management strategy that could improve nest success is habitat enhancement to increase elevation. This could include using dredge material or techniques to create dunes (Davis et al. 2001) to reduce overwash risk and increase success. Finally, we recommend incorporating coastal geomorphology data into conservation planning. Predicting future shoreline changes, and using vulnerability assessments to understand changes to critical habitat in light of sea level rise, increased storms and other stressors will allow managers to focus conservation efforts (McLeod et al. 2010, Sims et al. 2013, Jackson 2015). Proactive measures and continued research are critical to prevent declines, or continued range constriction of Wilson’s Plovers and other shorebird species.

Both the risk of predation and the risk of overwash influence the probability of nest success for Wilson’s Plovers, and changing environmental pressures could increase these risks. While overwash occurs less frequently, it is better predicted by habitat features than predation, which might indicate habitat cues could be more informative for birds making nest site selection choices that reduce overwash risk. However, predation remains a significant threat to the overall reproductive success of these species, influencing both nest success and often fledging success as well (Neuman et al. 2004, Pauliny et al. 2008). With a detailed assessment of how specific risks influence overall reproductive success, we can better understand nest success and the implications that changing habitat has on the ability of this species to adapt and persist, and how management can facilitate this.

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Table 3.1: Classification of community types, which were the categories within the covariate of community type for the overwash and predation components of the models. A total of 10 cover types were classified using literature, digitized orthophotos, and field observations. The percent of nests that were classified in each community type is also shown.

Cover Type	**Model Variable**	**Description**	**% of nests**
Active Dunes	Active_dune	Active building dunes, with plants such as beach elder (*Iva imbricata*), sea oats (*Uniola paniculata*) and beach croton (*Croton punctatus*). Usually primary dune ridge, just behind wrack line. Can be semi-permanent and well developed.	63.2
Dense *Spartina patens*	Dense_patens	Monoculture areas of *Spartina patens.*	2.2
Fiddler Crab Salt Pan	Fid_SaltPan	Open muddy areas with limited vegetation, dominated by fiddler crabs. May be near tidal creeks on back beaches, near beach ponds. Usually muddy substrates that get washed over on highest tides.	2.5
Inactive dunes	Inactive_dunes	Well established dunes, vegetated with species such as *Diodia teres, Eupatorium capillifolium*, *Conyza canadensis,* usually at least one or two primary dune ridges west of the ocean.	6.6
Interdune Meadow	Interdune_meadow	Low, vegetated areas, generally dominated by low growing plants, grasses and forbs such as *Phyla nodiflora, Sabatia stellaris, Cyperus retrorsus*.	6.1
Interdune Swale	Interdune_swale	Low areas, between dunes, not heavily vegetated, precursor to Interdune meadow.	6.9
Open beach	Open_beach	Open, non-vegetated sand above the tideline, but not beyond primary dunes.	3.1
Open sand	Open_sand	Open sand landward of the first primary dunes. Non-vegetated.	1.5
Overwash beach	Overwash_beach	Open beach that is frequently washed over. May be vegetated with high salt tolerant species, such as *Salsola kali*, *Borrichia frutescens*, and *Ipomoea pes-caprae*. Experiences tidal overwash on extreme tide events only. May be scoured by wind. Also may be exhibited as overwash fans. Early successional.	6.9
Salicornia	Salicornia	Patches of salicornia (*Salicornia virginica*) and sea purslane (*Sesuvium portulacastrum*). More vegetated than fiddler crab salt pans. Often found on back beaches, near inlets, and in areas with some level of tidal inundation. Generally low elevation.	1.2

Table 3.2: Complete model set compared using MCestimate, ranked with AIC_c. Overwash and predation risk are assessed with habitat or shoreline change variables included for each component, while the other component is held constant, as denoted by (.). A null model where both components are held constant is ranked for comparison.

	Model
Site Features Influencing Overwash Risk	overwashed(site)predated(.)
	overwashed(site+comm)predated(.)
	overwashed(site+comm+elev)predated(.)
	overwashed(site+comm+elev+marsh)predated(.)
	overwashed(site+comm+elev+marsh+tide)predated(.)
	overwashed(site+comm+elev+marsh+tide+up)predated(.)
	overwashed(site+elev)predated(.)
	overwashed(site+marsh)predated(.)
	overwashed(site+tide)predated(.)
	overwashed(site+up)predated(.)
	overwashed(site+tide+elev)predated(.)
	overwashed(site+up+elev)predated(.)
	overwashed(site+marsh+tide+up)predated(.)
Shoreline Change Rates Influencing Overwash Risk	overwashed(histSCR+site)predated(.)
	overwashed(histSCR+histTSCR+site)predated(.)
	overwashed(histSCR+histTSCR+EPRcurr+EPRSDcurr+site)predated(.)
	overwashed(EPRcurr+EPRSDcurr+site)predated(.)
	overwashed(histTSCR+site)predated(.)
	overwashed(EPRcurr+EPRSD+histSCR+site)predated(.)
	overwashed(EPRcurr+site)predated(.)
	overwashed(EPRSDcurr+site)predated(.)
	overwashed(EPRSDcurr+histTSCR+site)predated(.)
	overwashed(EPRcurr+histSCR+site)predated(.)
Site Features Influencing Predation Risk	overwashed(.)predated(site+inveg)
	overwashed(.)predated(site+inveg+comm+marsh)
	overwashed(.)predated(site+inveg+comm+marsh+tide)
	overwashed(.)predated(site+inveg+comm+marsh+tide+up)
	overwashed(.)predated(site+marsh+tide+up)
	overwashed(.)predated(site)
	overwashed(.)predated(site+comm)
	overwashed(.)predated(site+marsh)
	overwashed(.)predated(site+tide)
	overwashed(.)predated(site+up)
Null	overwashed(.)predated(.)

All variables are fixed effects: Site (site) = categorical (LSSI or CUIS), Elevation (elev) = continuous, Community (comm) = categorical (see Table 3.1), Distance to Marsh (marsh) = continuous, Distance to Tideline (tide) = continuous, Distance to Upland (up) = continuous, Current Shoreline Change Rate (EPRcurr) = continuous, Current Shoreline Change Standard Deviation (EPRSDcurr) = continuous, Historic Shoreline Change Rate (histSCR) = continuous, Historic Shoreline Change Standard Deviation (histTSCR) = continuous

Table 3.3: Top-ranked models (within delta 2AICc of top model) for each year, shown with the null model for comparison. Models were ranked using $\mathrm{AIC_c}$.

Year	**Model**	**$\mathrm{AIC_c}$**	**K**	**$\Delta\mathrm{AIC_c}$**	**w_i**
2012	Overwashed(site+elev) Predated(.)	861.59	4	0.00	0.46
	Overwashed(site+up+elev) Predated(.)	863.54	5	1.95	0.17
	Overwashed(site+comm+elev+marsh) Predated(.)	863.60	5	2.01	0.17
	Overwashed(.) Predated(.) **(null)**	912.58	2	50.99	0.00
2013	Overwashed(site+comm+elev) Predated(.)	850.72	11	0.00	0.53
	Overwashed(site+comm+elev+marsh) Predated(.)	851.92	12	1.20	0.29
	Overwashed(site+comm+elev+marsh+tide) Predated(.)	853.89	13	3.18	0.11
	Overwashed(.) Predated(.) **(null)**	872.57	0	21.85	0.00
2015	Overwashed(EPRcurr+site) Predated(.)	1007.21	4	0.00	0.14
	Overwashed(EPRStDevcurr+site) Predated(.)	1007.41	4	0.20	0.12
	Overwashed(EPRcurr+EPRSDcurr+site) Predated(.)	1008.75	5	1.54	0.06
	Overwashed(site) Predated(.)	1008.98	3	1.77	0.06
	Overwashed(EPRcurr+histSCR+site) Predated(.)	1009.18	5	1.97	0.05
	Overwashed(.) Predated(.) **(null)**	1009.23	2	2.02	0.05

Variables: Site (site) = categorical (LSSI or CUIS), Elevation (elev) = continuous, Community (comm) = categorical (see Table 3.1), Distance to Marsh (marsh) = continuous, Distance to Tideline (tide) = continuous, Distance to Upland (up) = continuous, Current Shoreline Change Rate (EPRcurr) = continuous, Current Shoreline Change Standard Deviation (EPRSDcurr) = continuous, Historic Shoreline Change Rate (histSCR) = continuous

Table 3.4: Coefficient estimates for the top-ranked model for each year for the overwash component of the models. The predation component that was best-ranked was the null model, and is not shown. Parameters with estimates that do not include zero in the 95% confidence interval are denoted with an asterisks (*).

Year	**Parameter**	**Estimate**	**SE**
2012	Intercept	1.28	1.54
	Site (LSSI) *	-1.07	0.38
	Elevation *	-2.5	0.94
2013	Intercept	-2.49	1.93
	Site (LSSI)	-1.02	0.84
	Dense Patens *	1.98	0.91
	Fiddler Salt Pan	-4.02	3.88
	Inactive Dunes	-3.49	2.97
	Interdune Meadow	0.27	1.22
	Interdune Swale	-4.01	11.5
	Open Sand	-2.09	2.13
	Overwash Beach *	2.74	0.9
	Elevation	-1.39	1.05
2015	Intercept	-9.7	1.06
	Site (LSSI)	0.79	1.43
	EPRcurrent *	0.05	0.03

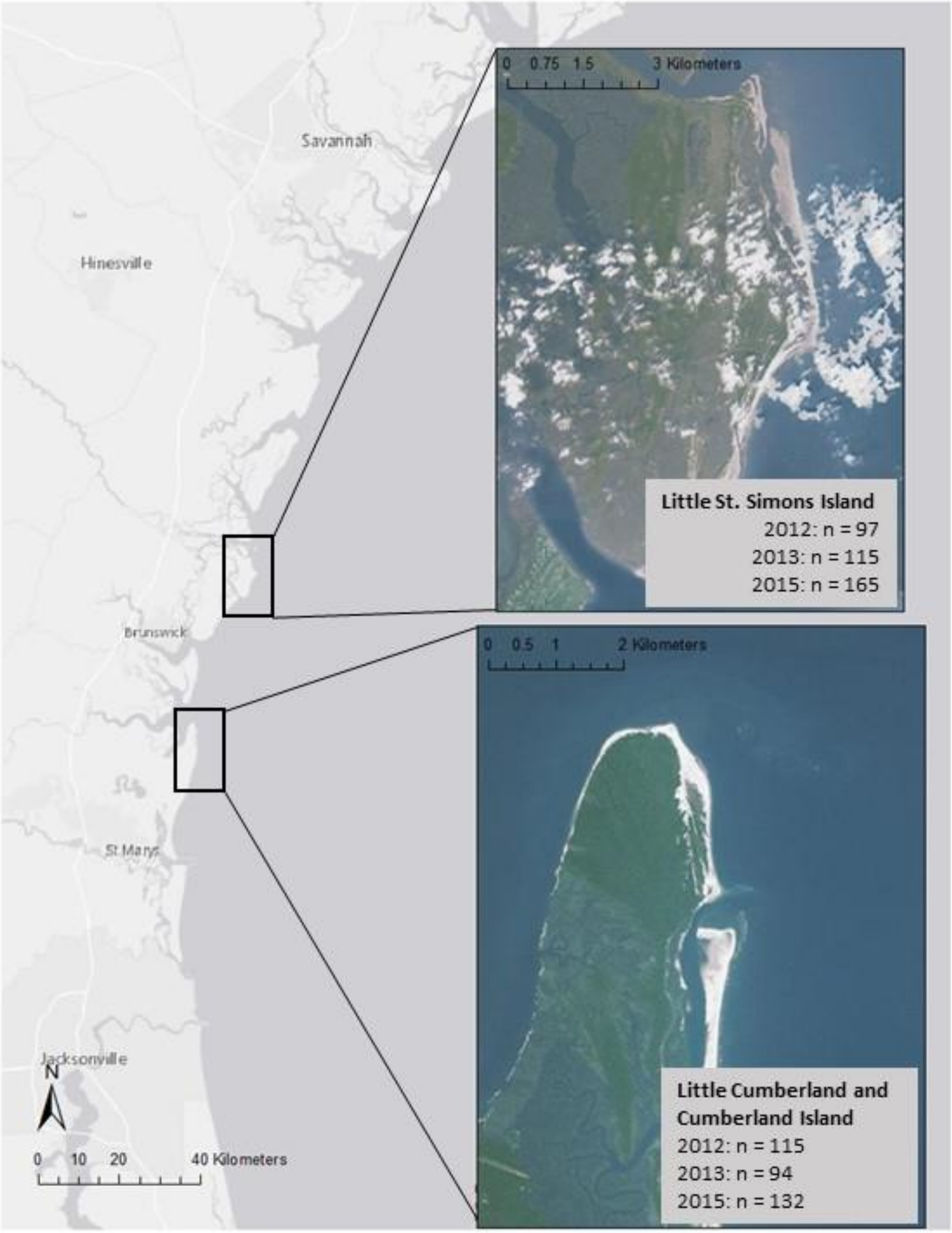

Figure 3.1: Study sites shown in relationship to position along the Georgia coast, with insets of Little St. Simons Island (LSSI) and Little Cumberland and Cumberland Island (CUIS). Nest numbers are totaled from the 2012, 2013 and 2015 field seasons, and shown inset with imagery of both islands.

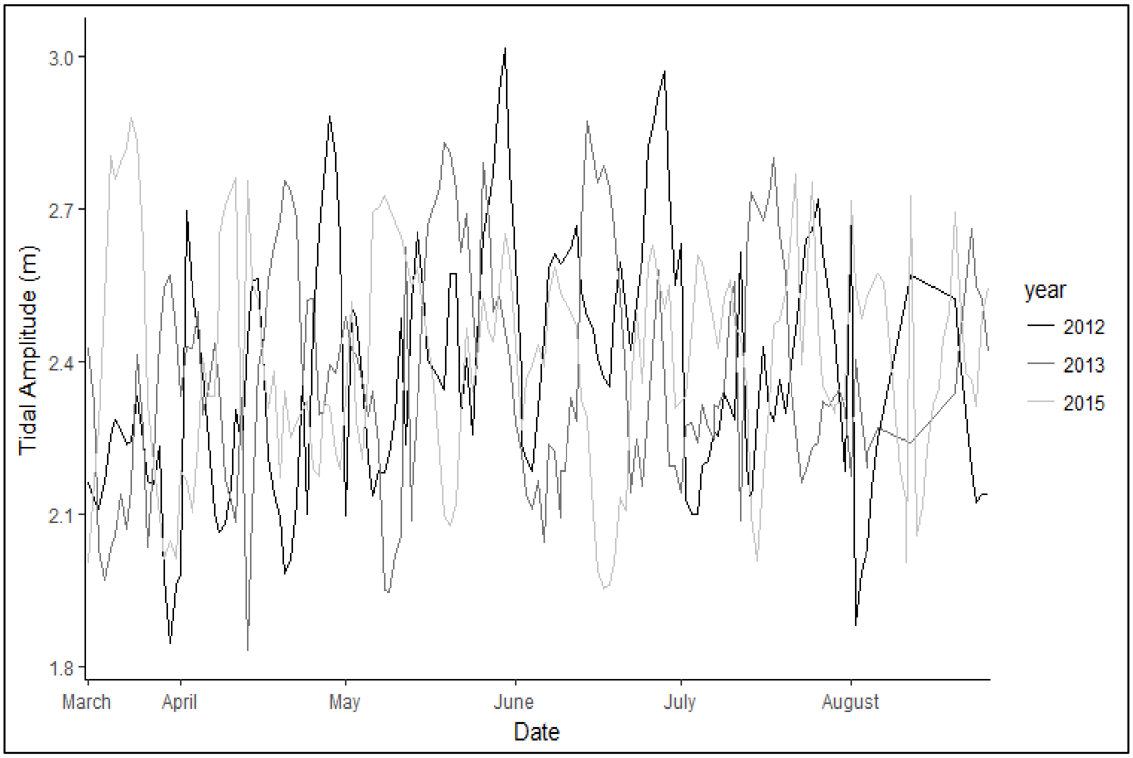

Figure 3.2: Daily maximum tidal heights during the Wilson's plover breeding season (March 15-August 1) taken from the Fort Pulaski, Georgia, NOAA tidal gauge station, for each year of the study. This figure shows the variability and recorded height of the tidal amplitude.

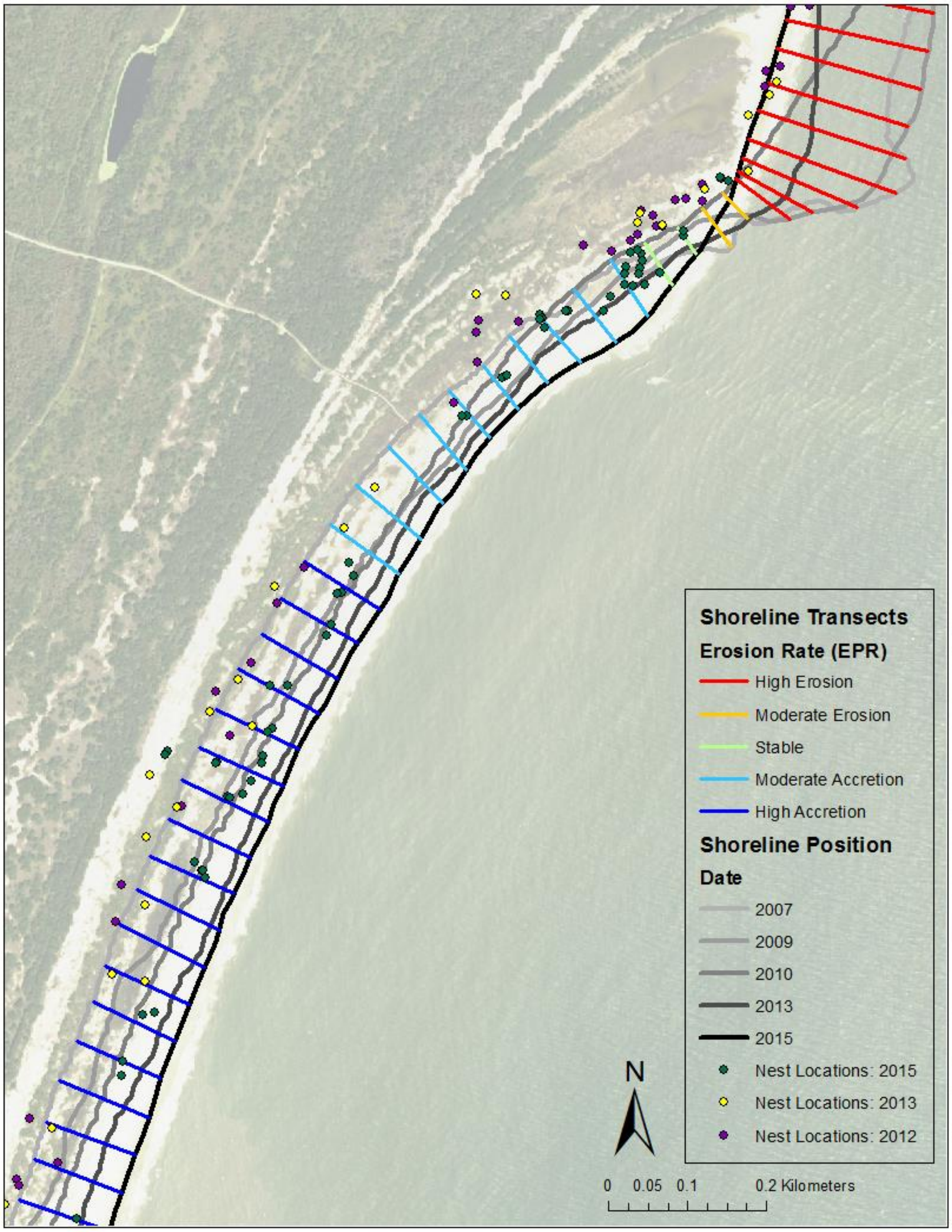

Figure 3.3: Map of a section of nesting habitat on Little St. Simons Island, Georgia. The projected transects, generated through an AMBUR analysis, which are used to calculate shoreline change are shown, categorized by color to indicate overall trend (erosional, stable, or accretional). Shorelines digitized for each year are shown as well, in gray, and Wilson's Plover nests are depicted as colored points on this map.

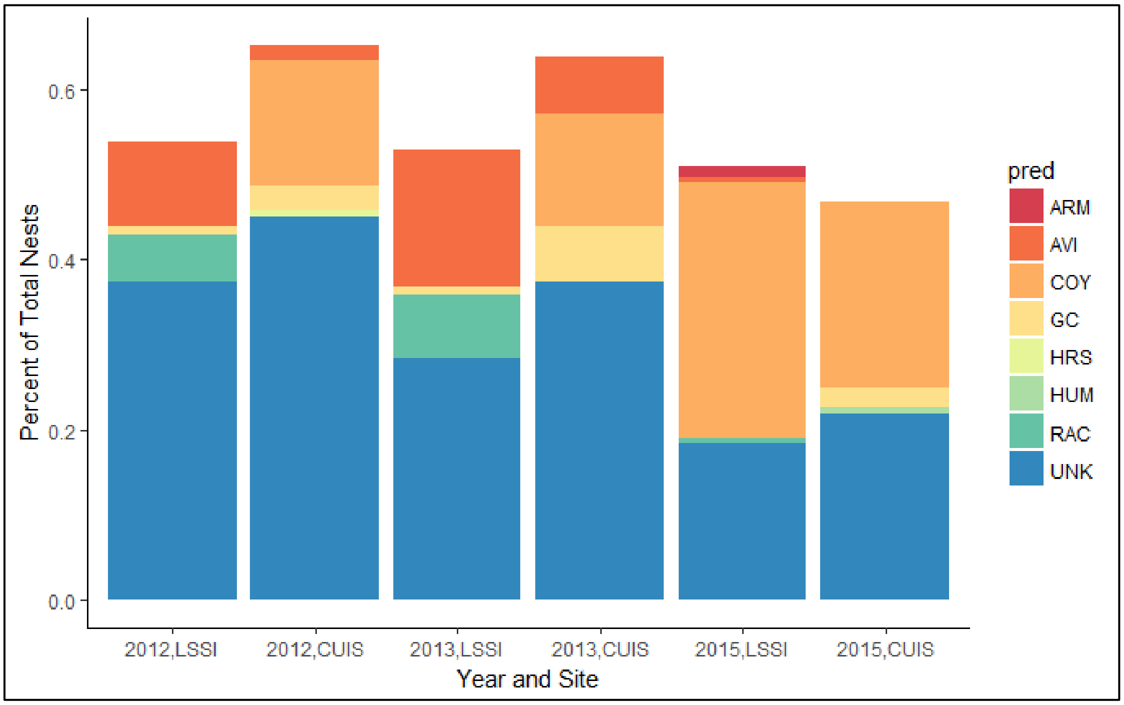

Figure 3.4: A summary of observed causes of nest predation by site and year. Unknown predators (UNK) could not be identified due to environmental conditions or a lack of physical evidence, and are shown in blue. Other nest predators are denoted by the following codes: ARM= armadillo, AVI= avian, COY= coyote, GC= ghost crab, HRS= horse, HUM= human, and RAC= raccoon.

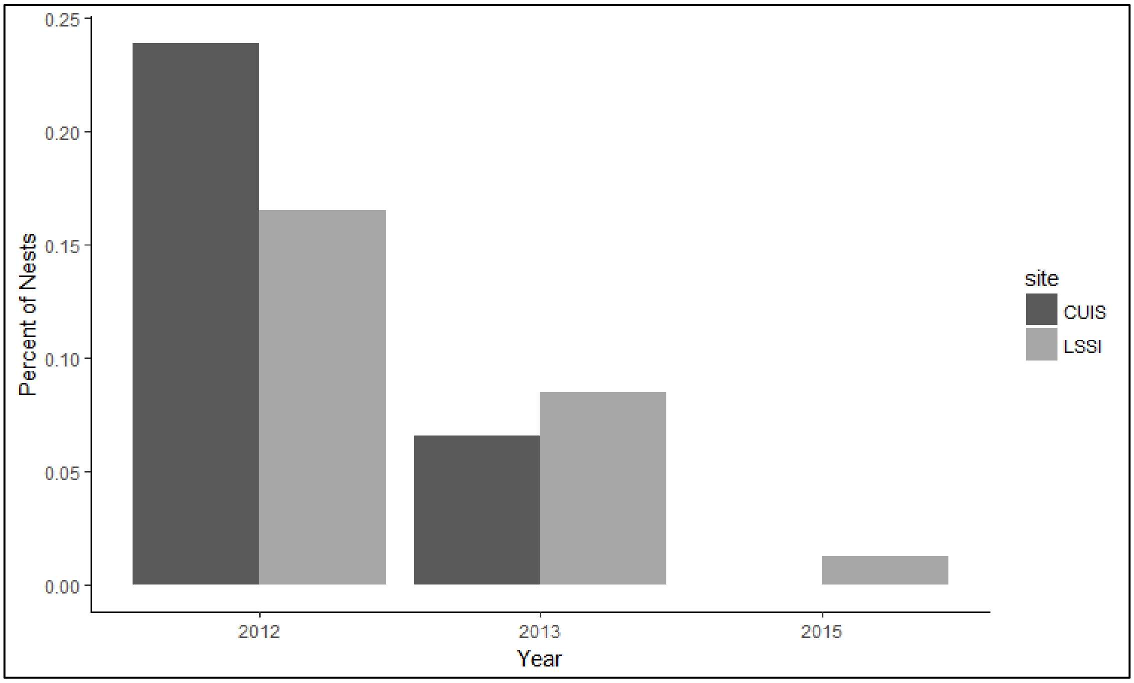

Figure 3.5: Percentage of observed nests that experienced tidal overwash, by year and site. Overwash failure varied by year, however in 2015, two nests failed due to overwash on LSSI while none failed due to overwash on CUIS.

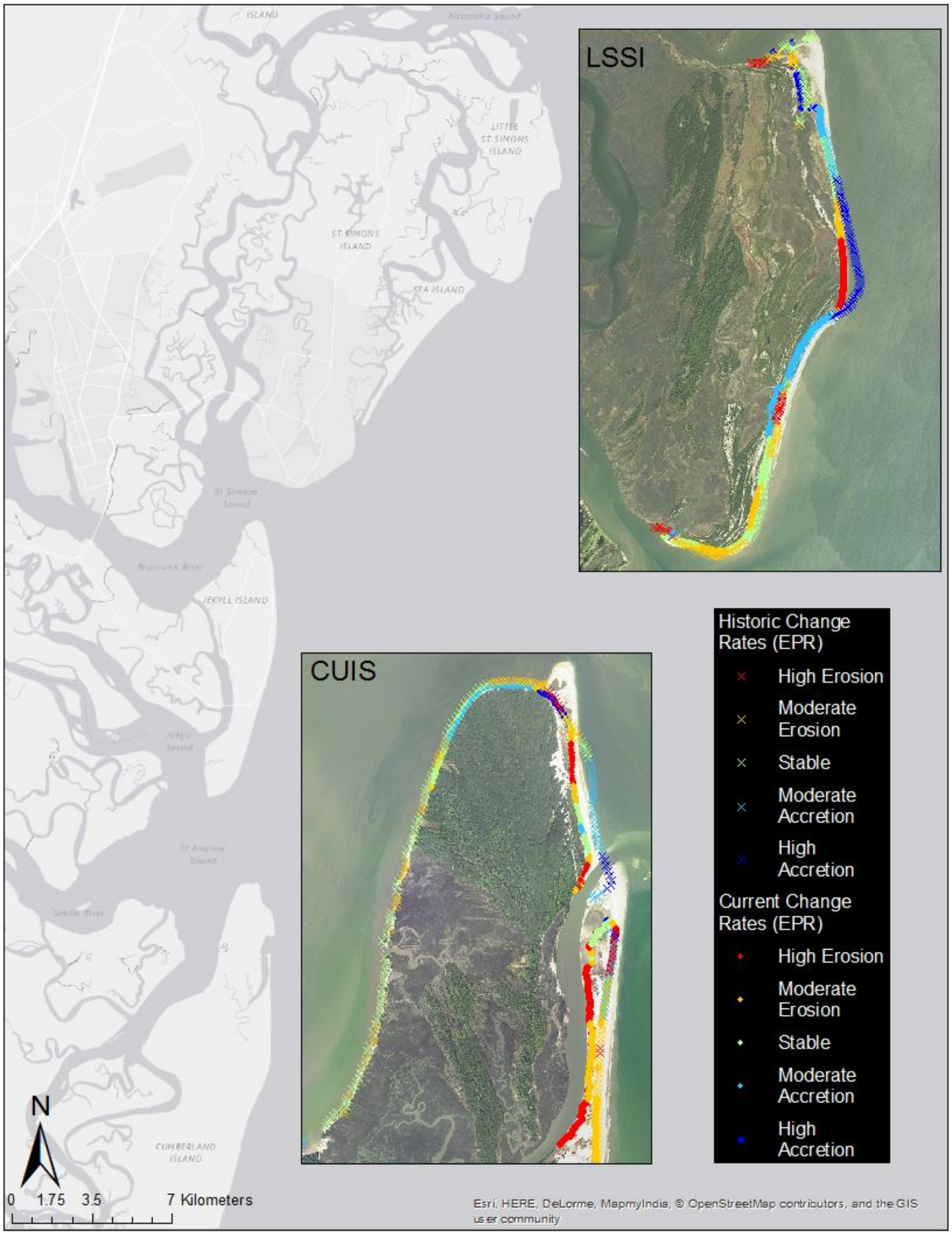

Figure 3.6: Shoreline change rates calculated through AMBUR shoreline analysis are shown at each of our study sites, Little St. Simons Island (LSSI) and Little Cumberland and Cumberland Island (CUIS). End point rates (EPR) of erosion are shown for the historic change data set (1800-2006) as an ‘x’ at each point, and a filled circle at each point for the current change data set (2007-2015). The colored scale shows rates of change, with erosion (negative EPR values) shown as red and orange, accretion (positive EPR values) shown in blue, and stable shorelines shown in green.

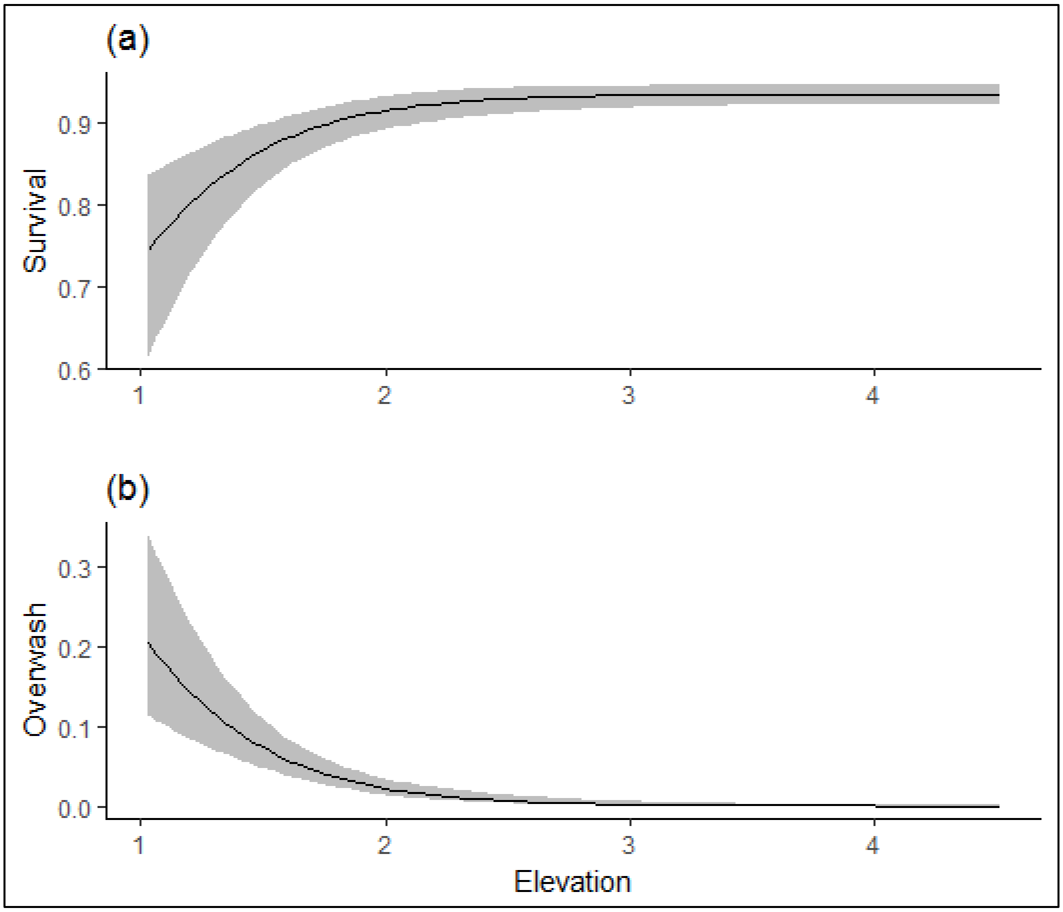

Figure 3.7: Daily predicted probability of survival (a) and overwash risk (b) for Wilson's Plover nests in 2012 on CUIS. These predictions are from our best-ranked model, which included the variables of site and elevation.

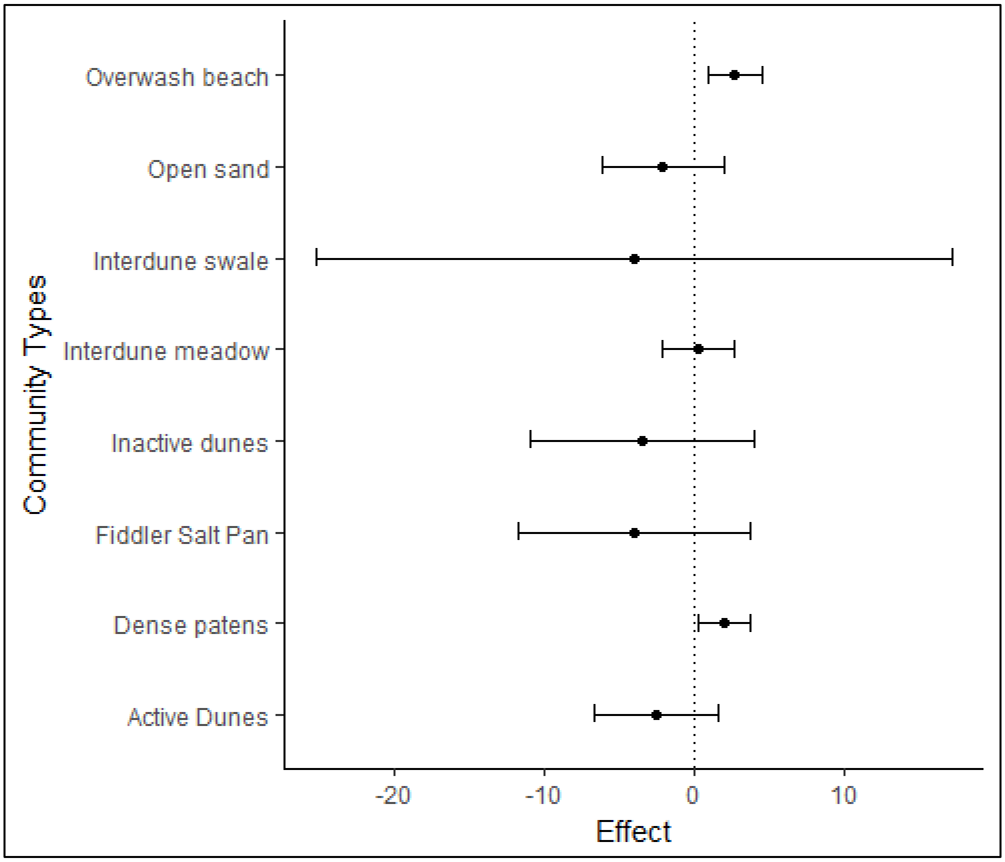

Figure 3.8: Effect size and 95% confidence intervals for all community types that influence the probability of a nest being overwash in 2013 on CUIS. Note that all the confidence intervals intercept zero, except for overwash beach and dense patens.

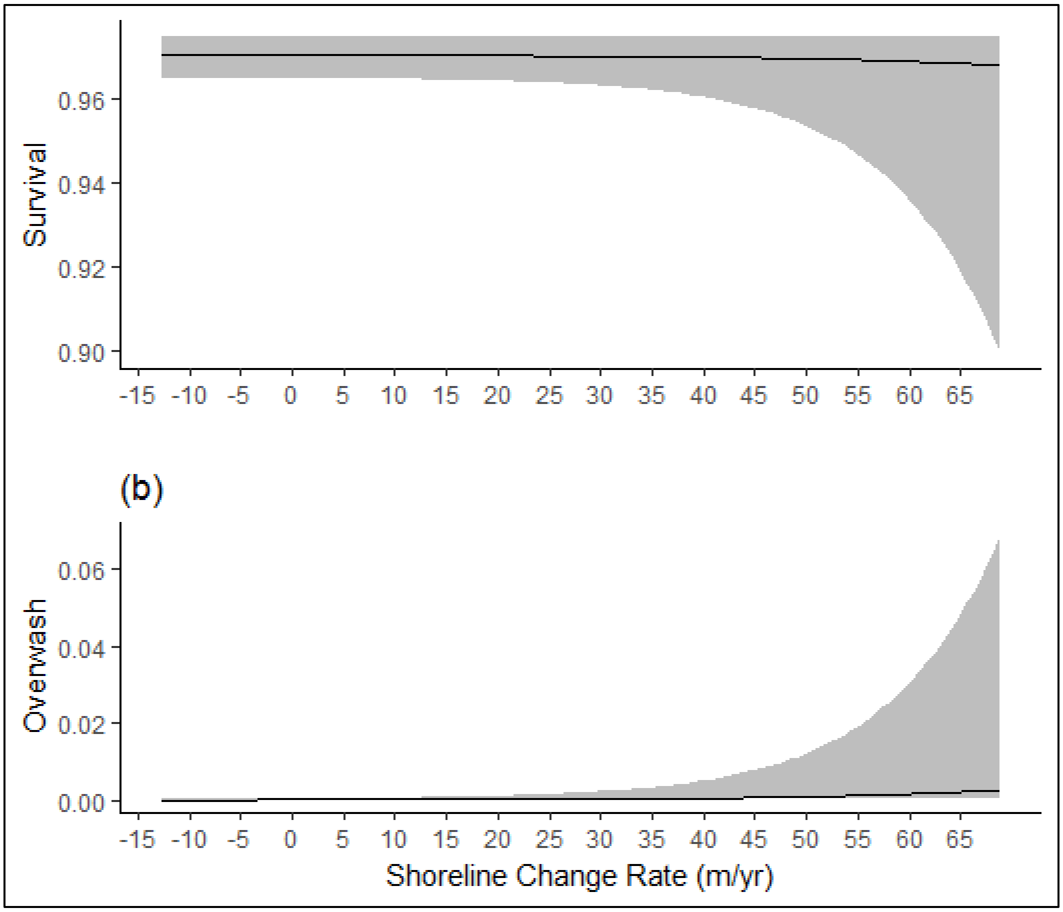

Figure 3.9: The effect of shoreline change rates on the probability of daily nest success (a) and daily nest failure due to tidal overwash (b) in 2015 on CUIS. These estimates were generated using the top-ranked model from the 2015 data set.

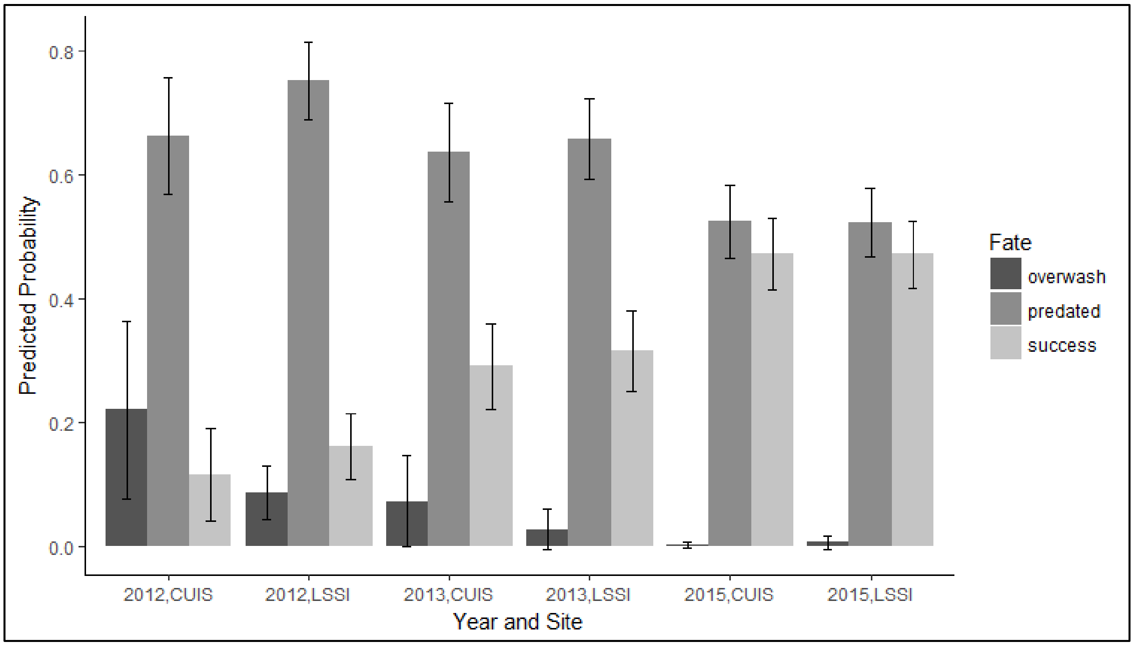

Figure 3.10: Predicted probability of overwash risk, predation risk and nest success, shown by site and year. Estimates are predicted using the top-ranked models from each year, and adjusted for each site. Error bars indicate the upper and lower 95% confidence interval of each estimate.

CHAPTER 4

THE INFLUENCE OF BIOTIC AND ABIOTIC FACTORS ON WILSON'S PLOVER CHICK SURVIVAL IN COASTAL GEORGIA[3]

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[3] A. V. Sterling, T. Keyes, S. D. Coleman, and R. J. Cooper. To be submitted to *Waterbirds.*

ABSTRACT

For nidifugous birds, fledging success – the probability that a hatched bird will survive to fledging – is a distinct life stage separate from nest success, and is equally important to nest success in determining the overall reproductive success of a population. Despite its importance, however, the survival of chicks to fledging is relatively understudied compared with nest success. Our objective was to estimate survival of Wilson's Plover (*Charadrius wilsonia*) chicks, as well as assess how several environmental factors influenced survival. Even at the site that produced the most chicks, daily survival was only 0.952 (SE=0.009), which over a 35-day fledging period became an overall survival rate of 0.290 (SE= 0.065). Overall, we found survival rates that were much lower than other published estimates, which is likely due to high predation rates. In particular, coyote (*Canis latrans*) predation was an important factor in the probability of chicks surviving to fledging. Of the abiotic factors, precipitation had a negative effect and tidal amplitude a positive effect on survival. Additionally, these results re-emphasize the necessity for predator management in closed, barrier island systems, in particular for the non-native coyote. This information is critical for future population demographics models as well as helping to fill knowledge gaps that exist within the breeding range of Wilson's Plovers.

INTRODUCTION

Both nest success – the probability of at least one egg hatching, and fledging success – the probability of a chick surviving until they are capable of sustained flight, are important components of the overall productivity of a population. Nests are usually monitored as the primary measure of productivity because they are stationary and easier to locate than mobile, precocial chicks. However, nest success does not always correspond to overall breeding success. Therefore, it is critical to understand fledging success rates, and how environmental factors influence those rates for species of conservation concern, such as declining shorebird species.

Many studies have shown that nest success alone is not a complete metric for understanding overall reproductive success (Cohen et al. 2009), and that nest survival often is less important than chick survival in population growth (Dinsmore et al. 2010). Management actions such as employing nest exclosures, or even head starting programs aimed at increasing productivity for shorebird species such as Piping Plovers (*Charadrius melodus*) and American Oystercatchers (*Haematopus palliatus*) have demonstrated that nest protection alone is not sufficient to increase reproductive output (Cohen et al. 2009, Collins et al. 2016). While these techniques mitigate some of the risks that influence nest success, such as predation, they do not impact the risks that precocial chicks face during the vulnerable, pre-fledging period; this highlights the importance of understanding chick survival as well as nest success when managing for shorebird productivity.

There are a number of risks that chicks face that could ultimately influence survival and overall productivity. Predation has been documented to be a leading cause of mortality for precocial chicks. Predation is especially relevant for shorebird chicks because they have a long pre-fledging period, when they are mobile but still vulnerable (Colwell et al. 2007, Cohen et al. 2009, Catlin et al. 2013, DeRose-Wilson et al. 2013). Additionally, the presence of novel predators could have a more significant effect on chick survival, and novel predators could impact certain life stages, such as nesting or fledging differently than native predators do (Harding et al. 2001). Environmental factors such as heavy precipitation and flooding due to tidal inundation influence chick survival rates as well (Groen and Hemerik 2002, Brudney et al. 2013). Additionally, changing climate will likely influence these risks (IPCC 2014), which could have significant implications at the population level. Assessing how these biotic and abiotic factors influence chick survival is particularly important for shorebird species of high conservation concern, such as the Wilson's Plover (*Charadrius wilsonia*).

The Wilson's Plover is considered threatened in the state of Georgia (GADNR 2015) and is a species of high conservation concern within the Atlantic Flyway (Brown 2013). Despite being considered a species of high priority for conservation action, there are significant knowledge gaps about the overall survival of chicks. While there are numerous studies that investigated nest success within the breeding range, there have not been many studies that have accounted for fledging survival for Wilson's Plovers (Bergstrom 1988, Corbat 1990, Hood 2006, Ray 2011). Although several published studies estimated productivity based on the number of observed fledglings, including one in North Carolina (Ray 2011) and one in Louisiana (Zdravkovic 2010), only one published study could be found estimating survival rates for Wilson's Plover chicks (DeRose-Wilson et al. 2013). Several management plans have highlighted this missing information as being critical to the conservation of the species (Brown 2013, Zdravkovic 2013).

To address these knowledge gaps, we estimated chick survival rates for Wilson's Plovers in Georgia using capture-mark-recapture models, and included several biotic and abiotic environmental factors that we hypothesized were important to overall survival of chicks. Predation was the leading biotic factor of interest. In particular, because one study site was sequentially invaded by a novel predator, the coyote (*Canis latrans*), over the period of study, we could indirectly assess the effect of this particular predator on chick survival. We hypothesized that predation pressure from this novel predator would negatively influence chick survival compared with years and/or sites without coyotes. We also incorporated several abiotic factors into our chick survival models, including precipitation, tidal amplitude and hatch date. We hypothesized that due to reduced thermoregulatory capacity, chick survival would decrease for individuals experiencing flooding due to increased precipitation and higher tides, and we hypothesized that chicks hatching early would be more likely to survive to fledging.

METHODS

Study Sites

During the 2012, 2013, and 2015 breeding seasons, from mid-March until late July, we monitored two sites that were composed of three barrier islands in coastal Georgia with previously known populations of breeding Wilson's Plovers (Corbat 1990, George and Schweitzer 2004, Sabine et al. 2006) . Little St. Simons Island (LSSI; ca. 31.26°N, 81.27°W; 5,260 ha) is a privately owned, undeveloped barrier island located in Glynn County at the southern branch of the Altamaha River Delta (Figure 4.1). It has approximately 11 km of wide, ocean-front beach with areas of tidal over-wash, preliminary and well-developed dunes with moderate vegetation, and areas of marsh ponds. There are two tidal creeks that bisect the beach to the Atlantic Ocean, and areas of marsh and mudflats that are accessible from the beach front. Cumberland Island National Seashore (CUIS; 30.85°N, 81.43°W; 14,736 ha), has approximately 29 km of beach, however we focused our efforts on the 4 km stretch of northern beach known as Long

Point. Included in this site is Little Cumberland Island (LCI; 30.97°N, 81.41°W; 2,300 ha), which is privately owned and separated from the larger island by a tidal creek. Both LSSI and CUIS serve as important nesting areas for shorebirds, sea birds and sea turtles (Schneider et al. 2010). They are generally composed of heterogeneous plant communities, including active primary dunes dominated by sea oats (*Uniola paniculata*) and beach elder (*Iva imbricate*) and overwash areas dominated by railroad vine (*Ipomoea pescaprae*) and sea purslane (*Sesuvium portulacastrum*)(Duncan 1982, Schoettle 1984). The backdune areas at these sites range from dense areas of *Spartina patens*, mud flats dominated by *Salicornia spp.*, and marsh dominated by *Spartina alterniflora*. Additionally, this is a dynamic habitat with areas of both significant erosion and accretion at these sites, and a tidal amplitude of nearly 3 meters (Davis 2004, Jackson 2010).

Nest Searching and Monitoring

Both sites were divided into thirds and we searched each section every third day to ensure adequate and even coverage and reduced disturbance. Nests were located through behavioral observations of adults, following tracks, and through systematic searches of all available nesting habitat (Powell 2001). Once found, nest locations were recorded using handheld Garmin GPSMAP 60CSx handheld units and monitored every three days throughout incubation. If a Wilson's Plover nest was found after clutch completion (three eggs in a nest, or two checks of only one or two eggs), eggs were floated (refer to Hood 2006 for floatation chart) to determine their approximate lay date to aid in banding of chicks (Hood 2006). A fate was assigned to each nest as either successful, when at least one egg hatched, or failed. Every effort was made to minimize disturbance. Searching and monitoring were carried out unless temperatures exceeded 38°C, winds exceeded 20 mph, or if heavy rain was falling. Due to these extraneous factors, if a beach section was missed on the scheduled day, monitoring resumed as soon as conditions permitted.

When a nest was within two days of expected hatch date, or if starring was observed on any egg within a clutch, the nest was checked daily. Chicks were captured by hand and banded at the nest with three colored plastic darvic bands and one colored plastic celluloid band, with two bands located on the tarsometatarsal region of each leg. In 2015, chicks were also banded with a metal USFWS band on the tibiotarsus. If chicks dispersed from the nest prior to capture and defensive adults were seen in the vicinity, we attempted to locate chicks through parental observations and by searching the immediate area. We banded chicks at 88.83% of the 197 nests that hatched during our study.

We systematically searched for marked chicks by foot and bicycle from April 27 until August 1 in all potential suitable habitat, including front and back beaches, and used spotting scopes to resight chicks. To ensure complete coverage of both sites, observation periods for resighting chicks were condensed to six, six-day intervals, to standardize survey effort and account for weather days. We resighted chicks for a total of 36 days after the hatch date, at which point the chick was considered fledged. Estimates for age of fledging vary for Wilson's Plovers from 29 days in North Carolina (Ray 2011), to up to 35 days in Louisiana (Zdravkovic 2010). In cases where chicks experience limited disturbance and abundant food and cover resources, fledging may be delayed (Zdravkovic 2013), so we considered survival to day 36 as fledged. Chicks that hatched after June 27 were censored from this analysis because resighting efforts ended before these individuals reached day 36.

Biotic and abiotic variables

In addition to the resighting data collected for each chick, we also included biotic and abiotic variables in our survival models. These data included the presence of coyote nest predation as a binary factor, which occurred in all years at CUIS, but only in 2015 at LSSI. In 2012 and 2013, while there were coyotes present on LSSI, there was no observed nest predation due to coyotes among any beach nesting bird species that were monitored, including American Oystercatchers (*Haematopus palliatus*), Least Terns (*Sternula antillarum*), and Black Skimmers (*Rynchops niger*). Therefore, we concluded that during 2012 and 2013, birds nesting on LSSI did not experience coyote predation pressure. Therefore, chicks hatched on LSSI in 2012 and 2013 were assigned a 0 for this variable, while chicks hatched on CUIS in 2012, 2013, and 2015, as well as chicks hatched on LSSI in 2015 were assigned a 1 for this variable. We also included abiotic variables of hatch date, the sum of the precipitation that fell during each chick's prefledging period, and the highest tide experienced by each chick during the prefledging period. We included hatch date in our models, because other studies have shown that this has a significant influence on chick survival, where early hatching nests have a higher probability of producing fledged chicks (Brudney et al. 2013, Catlin et al. 2013). Hatch date was calculated for each chick using Julian date. Heavy precipitation has been shown to decrease survival of Piping Plover chicks, particularly for young chicks which are unable to thermoregulate well (Brudney et al. 2013). Additionally, a previous study found that flooding of Piping Plover habitat on the Missouri River during water release periods resulted in some chicks being washed away, and although it was uncommon for the entire nesting habitat to be inundated, this potentially resulted in decreased survival (Catlin et al. 2013). Precipitation information was collected at the weather station on Sapelo Island (identification GHCND:US1GAMI0002) by NOAA (https://www.ncdc.noaa.gov/cdo-web/), which is located approximately 50 km north of LSSI. Maximum tidal height in meters above the North American Veritcal Datum of 1988 (NAVD 88) was gathered from the Fort Pulaski NOAA tidal gauge station (http://tidesandcurrents.noaa.gov/) located approximately 100 km north of LSSI.

Analytical Methods

To estimate apparent survival (φ) and detection parameters (*p*), we used a Cormack-Jolly-Seber model in the R version 3.2.3 (R Development Core Team 2015) package RMark (Laake 2013) to construct models for program MARK (White and Burnham 1999), which allowed us to incorporate biotic and abiotic variables into models. We used the median c-hat test on the global model in Program MARK to estimate and correct for overdispersion, and the quasi-likelihood Akaike’s Information Criterion corrected for small sample size (QAICc) to rank models for survival analyses (Burnham 2002) assess significance of the environmental variables (DeRose-Wilson et al. 2013).

We estimated survival rates using six encounter intervals that were each six days long. We did not incorporate observations beyond day 36, at which point we assumed chicks were capable of flight. Due to modeling constraints because of the scarcity of our observations, we held survival constant, but allowed resight rates to vary with time. We allowed survival to vary using site and coyote predation as groups, and allowed detection to vary by observer and site, but combined data from all three years for analysis. We also included models that incorporated the influence of hatch date, total precipitation, and height of highest tide on survival rates as continuous, individual covariates for each chick. We included an intercept-only model where both survival and detection were held constant, as well. We built a total of 16 models, including the intercept-only model and a global model with the additive effects of all the variables incorporated to estimate the influence of weather and predation risk on chick survival (Table 4.1). Model covariates whose 95% confidence limits did not include zero were considered to be statistically significant in our results. Finally, we raised the predicted survival estimate from the best ranked model to the sixth power to calculate the survival rate for the entire period from hatch until fledging (Powell 2007).

RESULTS

We monitored a total of 635 nests over the three breeding seasons among all sites that were either successful or failed prior to the June 27 hatch date. Of these nests, 197 hatched, for an apparent success rate of 0.31. From these successful nests, we banded a total of 371 chicks with unique color band combinations. We resighted chicks in both front and back beach habitats, and while we saw chicks below the tideline feeding with adults, we also observed them frequently at beach ponds, in overwash areas, in dense vegetation and on exposed mud flats.

Our top model, the global model, was more than Δ2 QAICc units above the next model and it included all the covariates for the survival estimate and time and observer for detection, so we used this model to calculate predictions (Table 4.1). However, the four top models that accounted for more than 96% of the weight all included every survival covariate, and only varied by the influence of different covariates on detection. Therefore, we did not feel that model averaging was necessary, because in this study our primary concern was estimating survival.

For chicks at LSSI, during years when no coyote predation was observed, we estimated a 0.781 (95% CI= 0.712-0.85) survival probability for the six-day observation period (Table 4.2). On LSSI, in the years without coyote predation, the survival estimate for the entire fledging period of 36 days, was 0.290 (95% CI=0.162-0.418). That rate dropped significantly when coyote predation was observed on LSSI to a 0.459 (95% CI= 0.335-0.584) survival probability per period, and only a 0.020 (95% CI= -0.007-0.048) probability of surviving to fledging. This rate was comparable to CUIS, which had coyote predation pressure all three years. Chicks on CUIS had a 0.520 (95% CI= 0.453-0.586) probability of surviving a six-day observation period, and an overall fledging survival probability of 0.038 (95% CI= 0.014-0.062). Detection was significantly influenced by both observer and time, and detection ranged from a mean over the six periods of 0.138 (95% CI= 0.003-0.646) for the worst observer, to 0.702 (95%CI = 0.417-0.802) for the best observer (Figure 4.2).

Our top model included all the biotic and abiotic covariates for predicting survival. The presence of coyote predation (β=-1.433, 95%CI=-2.137- -0.729), and the sum of precipitation experienced (β=-0.582, 95%CI=-0.910- -0.254) had significant negative effects on survival, while the highest tidal amplitude experiences had a significant positive effect on survival (β=0.291, 95%CI=0.016-0.566). The other covariates of hatch day and site were not significant (Table 4.3). We used the top model to predict survival for covariates that were significant, and included the influence of coyote predation for visual comparison. We saw significantly lower predicted survival rates for sites with coyote predation, however there was not a significant difference between CUIS and LSSI in 2015, which was when coyote predation of nests was observed at both sites (Figure 4.3). Precipitation negatively influenced survival (Figure 4.4), while tidal amplitude had a positive effect on chick survival (Figure 4.5).

DISCUSSION

Overall, we found survival rates that were much lower than other published estimates, which is likely due to high predation rates. With our results, we were able to show that coyote predation is a significant factor in the probability of chicks surviving to fledging. We also found that abiotic factors influenced survival, however our models were constrained by our ability to detect chicks frequently and easily within the expansive area we were monitoring. Although we did not quantify spatial use of the landscape, we did observe family units moving distances of up to one kilometer in a single day and on several occasions chicks were observed traversing *Spartina* marshes and crossing swift moving tidal creeks. These observations could help explain why detection rates were so low, and illustrate the importance of monitoring the entire potential nesting area for chicks, which we feel we accomplished with this study. Our results also indicate the need to incorporate more spatial covariates into models, and attempt to better quantify habitat use in future studies. Regardless, this first attempt to estimate chick survival on the Georgia coast does fills knowledge gaps and will be useful in future population models which can help inform management actions.

Our chick survival estimates were significantly lower than estimates from North Carolina, where the daily survival for Wilson's Plover chicks was estimated at 0.995 (DeRose-Wilson et al. 2013). In our study, even at our most productive site, daily survival was only 0.952 (SE=0.007), which over a 36-day fledging period is 0.226 (SE= 0.061; Table 4.2). This low chick survival estimate for Wilson's Plovers also mirrors the lower rates of success that have been documented when comparing the productivity of sympatric shorebird species in Georgia to sites in other states. American Oystercatchers, which have been closely monitored in Georgia, show both reduced nest success and the lowest fledging productivity rates when compared to other areas within the Atlantic coast breeding range (Nol and Humphrey 2012). The causes for reduced productivity in Georgia are usually attributed to a combination of tidal overwash due to the large tidal amplitudes, and predation (George 2002, Sabine et al. 2006). Prior to coyote invasion, the main mammalian predator responsible for chick mortality was likely the raccoon, although avian predation can also be significant (Corbat 1990, Corbat and Bergstrom 2000). However, with the invasion of coyotes on LSSI, Wilson's Plover chick survival plummeted to almost zero.

Abiotic factors such as precipitation, temperature, and tidal flooding have also been shown to be significant risk factors for precocial chicks (Colwell et al. 2007). We predicted that the amount of rainfall and tidal flooding would decrease chick survival due to their limited thermoregulatory capacity, and while our results suggested this was true for the amount of precipitation, we saw that tidal amplitude had a positive effect on chick survival. High tides do decrease nest success, and tidal overwash is one of the leading causes of nest failure at these sites (Chapter 2), however chicks are likely mobile enough to avoid high tides. Rather than pose a risk, tidal overwash events maintain nesting habitat (DeRose-Wilson et al. 2013) and may increase food availability. Previous studies have shown that flooded substrates increase invertebrate abundance at Piping Plover chick foraging areas along the Missouri River (Le Fer et al. 2008) and that tidal flooding replenishes microphytobenthos, which feeding fiddler crabs glean from the substrate

(Ribeiro and Iribarne 2011), thereby increasing abundance of crabs available to Wilson's Plover chicks. Increased food resources influence growth rates for chicks, possibly reducing the time to fledging which allows chicks to avoid threats, and increasing overall survival (Catlin et al. 2013). The relationship between food resources, growth, and survival underscores the importance of incorporating environmental factors into chick survival models.

Aside from precipitation and tidal amplitude, there are several other factors that we did not include in our models that likely have an influence on chick survival, and should be considered in future research. In this study, we did not include spatial information, especially the association of feeding areas with survival. Results from studies that have focused on chick survival in other plover species have suggested that movement and location of foraging sites greatly influences overall survival (Colwell et al. 2007, Cohen et al. 2009). However, our study lacked fine scale movement data for chicks, which should be a focus for future research, especially as new technology for tracking very small individuals becomes available. Additionally, incorporating broader climatic effects, such as temperature extremes, could also be important as these have been shown to influence chick survival in other precocial species (Tyler and Green 2004), and could become more relevant with increasing unpredictability due to climate change (van de Pol et al. 2010b). Due to technological, logistic, and modeling constraints we could not include additional factors into our models, but recommend future research to focus on these aspects in modeling chick survival.

Aside from environmental factors, another component that influences survival of chicks is age, but because of low detection and therefore sparse resighting of banded chicks, we were not able to include time-varying survival in our models. It has been shown that survival of shorebird chicks is lowest during the first week of life, and as precocial chicks become more mobile they are better able to avoid threats and navigate the landscape, thereby becoming less vulnerable to risks such as predation and flooding (Hitchcock and GrattoTrevor 1997, Colwell et al. 2007). However, this high level of mobility likely reduced our overall ability to detect chicks. In our study, to meet the assumption of our models (no animals emigrating and then reentering the study area) it was necessary to monitor the entire beach, because chicks are highly mobile and physical boundaries (such as tidal creeks and *Spartina* marshes) were not barriers to movement. Monitoring a smaller area could have increased detection, which would have made our models more robust to additional covariates. However, at our site we could not restrict the search area without violating closure assumptions. Alternate analysis techniques that use radio transmitters on adults to estimate survival of unmarked young could be useful in rectifying the low or imperfect detection issues that we had due to monitoring such an expansive field site, and have been used successfully to estimate Mountain Plover (*Charadrius montanus*) chick survival (Lukacs et al. 2004).

One final caveat of our study is that chick survival was estimated for each individual chick, even though individuals are part of a brood. The average clutch for Wilson's Plovers is three eggs, and after hatching, adults and chicks feed and move together (Corbat and Bergstrom 2000). Although chicks do move as a family unit, a recent study that closely tracked Mountain Plover chicks through pre-fledging suggested that survival rates varied independently for each chick (Lukacs et al. 2004). Once chicks are mobile, they face threats such as predation, which operates at an individual scale, rather than on the whole brood. Therefore, in this case, we maintain that chicks are operating as individuals rather than as a unit, and the independence assumption for our models is not violated.

This research provides the first survival estimates for Wilson's Plover chicks on the Sea Islands along the southeastern U.S. coast, which has been identified as an important area for the global population of this species (Zdravkovic 2013). The sites included in our study, CUIS and LSSI, provide some of the most important breeding areas in the state, although our findings suggest low predicted survival for chicks. Both the biotic factor of coyote predation and the abiotic factors of precipitation and tidal flooding had significant effects on survival of chicks. These results show that years with more precipitation may be less successful for Wilson's Plover chicks; frequency of erratic and heavy rainfall is expected to increase under changing climate regimes (IPCC 2014) and therefore these changes might have significant implications for overall reproductive success. Additionally, these results highlight the importance of reducing disturbance, either due to monitoring or recreational activities, during periods of heavy precipitation, especially in areas with young chicks (Brudney et al. 2013).

These survival estimates also highlight the importance of predator management to increase not only nest success but chick survival as well. Prior to coyote invasion, removal of raccoons was necessary to maintain adequate shorebird productivity on LSSI. As coyotes become established on the Sea Islands, it becomes clear that without some sort of management the persistence of populations of beach nesting birds such as Wilson's Plovers will be severely jeopardized. This could be especially relevant because novel predators such as coyotes might influence certain reproductive stages, such as nesting or fledging, differently than previously established predators. Finally, these results emphasize that reproductive output is best measured by not only monitoring the number of successful nests in a given area, but the number of chicks that survive to fledging. For nidifugous species such as shorebirds, targeted short-term management during the pre-fledging period could be especially effective at increasing overall reproductive success, given the short and discrete period of time that chicks are unable to fly (Dinsmore et al. 2010). Our estimates of these parameters fill several knowledge gaps and can contribute to future modeling efforts that will yield better management for overall reproductive success, and increased understanding of demography of the population.

LITERATURE CITED

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Table 4.1: Complete set of Cormack-Jolly-Seber models estimating 6-day period survival (φ) and detection (p) for Wilson's Plover chicks at LSSI and CUIS, GA in 2012, 2013 and 2015. Models are ranked using QAIC_c and ordered from best-ranked to worst.

Model[a]	K[b]	QAICc[c]	ΔQAICc[d]	w_i[e]	Quasi-deviance
(ϕ)hatch + coy pred + high tide + precip + site (p)time+ obs	14	588.85	0.00	0.61	560.10
(ϕ)hatch + coy pred + high tide + precip + site (p)site+ time+ obs	15	590.96	2.11	0.21	560.10
(ϕ)hatch + coy pred + high tide + precip + site (p)time	11	592.72	3.87	0.09	570.25
(ϕ)hatch + coy pred + high tide + precip + site (p)site+ time	12	593.63	4.78	0.06	569.07
(ϕ)coy pred (p)site + time	8	595.84	6.99	0.02	105.93
(ϕ)coy pred + site (p)site + time	9	597.83	8.98	0.01	105.85
(ϕ)site (p)site + time	8	608.13	19.28	0.00	118.22
(ϕ)high tide + site (p)site + time	9	608.64	19.79	0.00	590.33
(ϕ)hatch + site (p)site + time	9	608.96	20.11	0.00	590.64
(ϕ)precip + site (p)site + time	9	609.70	20.85	0.00	591.38
(ϕ)hatch + coy pred + high tide + precip + site (p)~1	7	614.48	25.63	0.00	600.28
(ϕ)high tide (p)site + time	8	614.76	25.91	0.00	598.50
(ϕ)hatch + coy pred + high tide + precip + site (p)site	8	616.30	27.45	0.00	600.04
(ϕ)hatch (p)site + time	8	620.40	31.55	0.00	604.15
(ϕ)precip (p)site + time	8	620.71	31.86	0.00	604.46
(ϕ)constant (p)constant **(null)**	2	649.18	60.33	0.00	171.50

[a] Hatch = number of days after 1 January that a chick hatched, coyote predation = 0 (no coyote predation pressure) or 1(coyote predation pressure), high tide = highest tidal amplitude experienced by chick during prefledging, precip = total amount of precipitation experienced by a chick during prefledging, site = Little St Simons Island or Cumberland Island, obs = observer

[b] Number of parameters in each model.

[c] Akaike's Information Criterion corrected for small sample bias and overdispersion

[d] Difference between top-ranked model and subsequent model

[e] Weight of evidence for the relative support for each model

Table 4.2: Survival rates predicted from top Cormack-Jolly-Seber model, for six-day observation period, daily survival rates, and fledging survival rates (6 periods, totaling 36 days).

Site	Coyote Predation	Period Survival[a]	Period SE	95% LCL	95% UCL	Daily Survival[b]	Daily SE[c]	Fledging Survival[d]	Fledging SE[e]	Fledging 95% LCL	Fledging 95%UCL
LSSI	No	0.781	0.035	0.712	0.85	0.952	0.007	0.226	0.061	0.107	0.346
LSSI	Yes	0.459	0.064	0.335	0.584	0.878	0.02	0.009	0.008	-0.006	0.025
CUIS	Yes	0.52	0.034	0.453	0.586	0.897	0.01	0.02	0.008	0.005	0.035

[a] Period Survival = six-day observation period, estimated from the top CJS model, ($\hat{S}_p$).

[b] Daily Survival = calculated as $\sqrt[6]{\hat{S}_p}$, using delta method (Powell 2007).

[c] Daily SE = calculated as $\sqrt{\left(\frac{1}{36} * \widehat{var}(\hat{S}_p) * \sqrt[6]{\hat{S}_p}^{10}\right)}$,using the delta method (Powell 2007).

[d] Fledging Survival = calculated as $\hat{S}_p{}^{6}$, to estimate survival across all six observation periods.

[e] Fledging SE = calculated as $\sqrt{(6^2 * \widehat{var}(\hat{S}_p) * \hat{S}_p{}^{6})}$,using the delta method (Powell 2007).

Table 4.3: Parameter estimates, 95% confidence intervals and standard errors from the best Cormack-Jolly-Seber model predicting Wilson's Plover chick survival on LSSI and CUIS, GA. Significance as determined by a confidence interval that does not overlap zero is indicated with an asterisk (*).

Variable	Parameter Estimate	Lower 95% CL	Upper 95% CL	SE
(ϕ) Intercept	1.51	0.81	2.22	0.36
(ϕ) Hatch	0.22	-0.02	0.46	0.12
(ϕ) Coyote Predation *	-1.43	-2.14	-0.73	0.36
(ϕ) High Tide *	0.29	0.02	0.57	0.14
(ϕ) Precipitation *	-0.58	-0.91	-0.25	0.17
(ϕ) site: LSSI	-0.24	-0.78	0.30	0.28

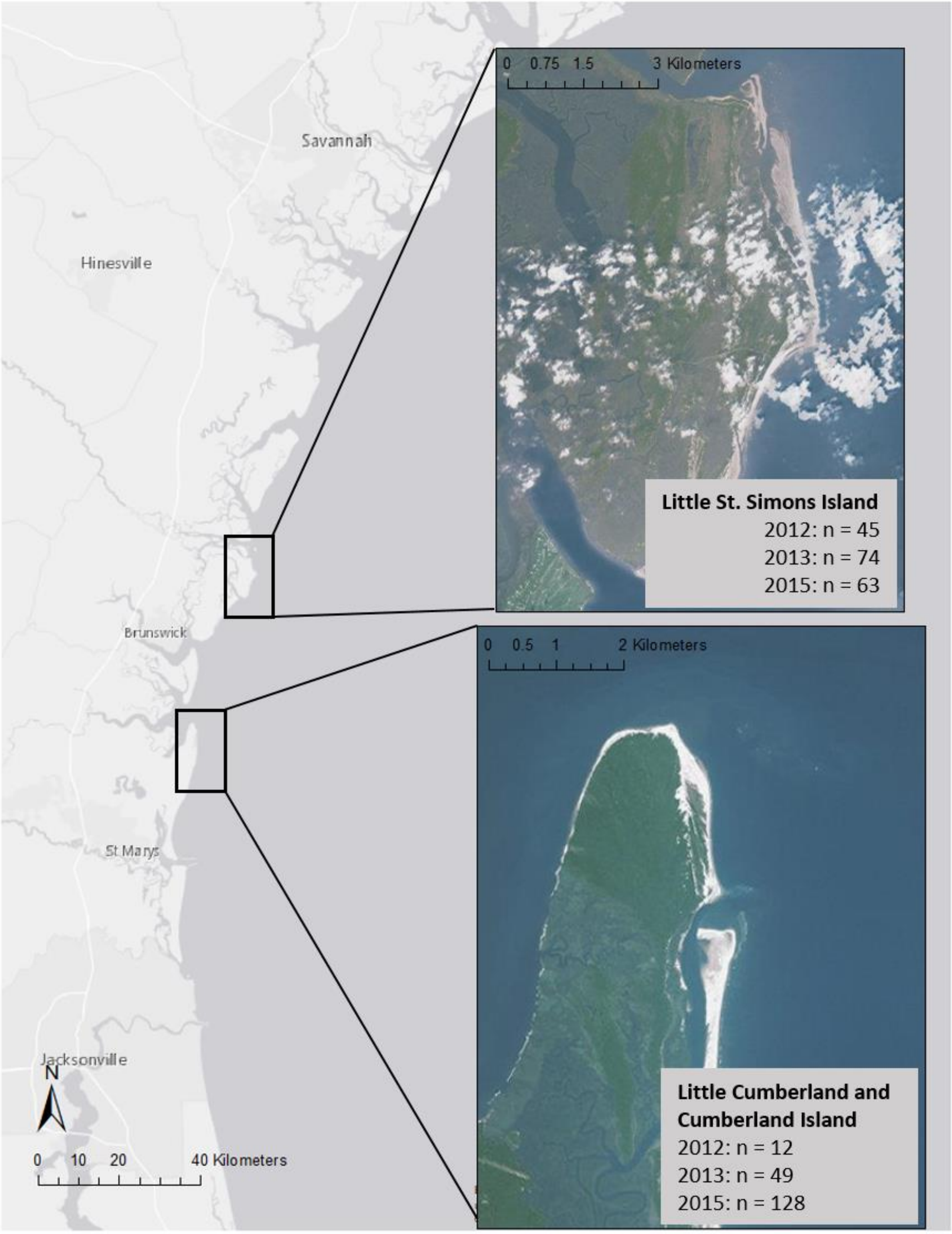

Figure 4.1: Study areas shown in relationship to position along the Georgia coast. Number of banded Wilson's Plover chicks that were included in this analysis are shown by year, inset with imagery of both islands.

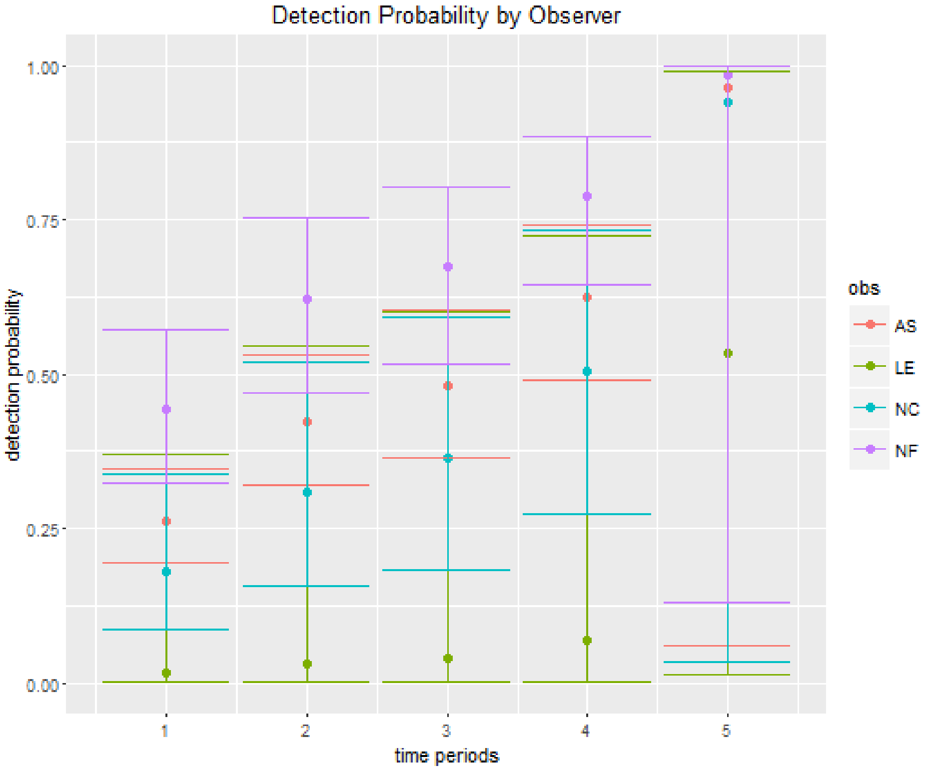

Figure 4.2: Estimates of detection of Wilson’s Plover chicks over six-day time periods, varying by observer and alpha-coded to match individual observers. Points are the mean detection with a 95% confidence interval shown as bars. Detection increases over time, with variation by observer in terms of both mean and variance.

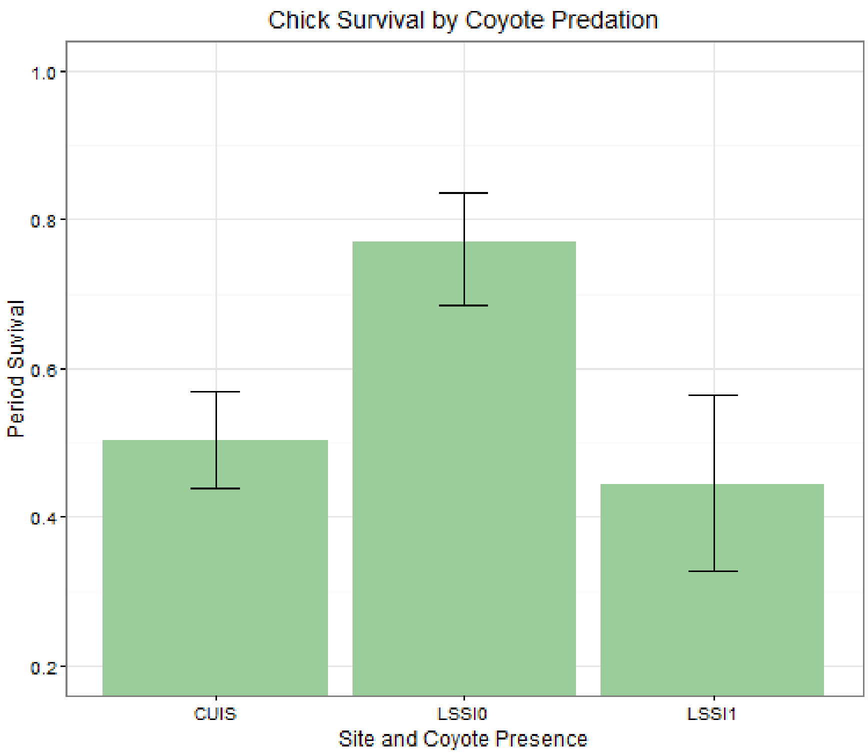

Figure 4.3: Predicted Wilson's Plover survival from top Cormack-Jolly-Seber model showing the effect of coyote predation pressure on period survival for chicks. Cumberland Island (CUIS) experienced coyote predation during the 2012, 2013 and 2015 nesting seasons, while Little St Simons had no coyote predation during 2012 and 2013 (LSSI0), but did experienced coyote predation in 2015 (LSSI1). Bars show mean predicted survival with error bars indicating 95% upper and lower confidence intervals.

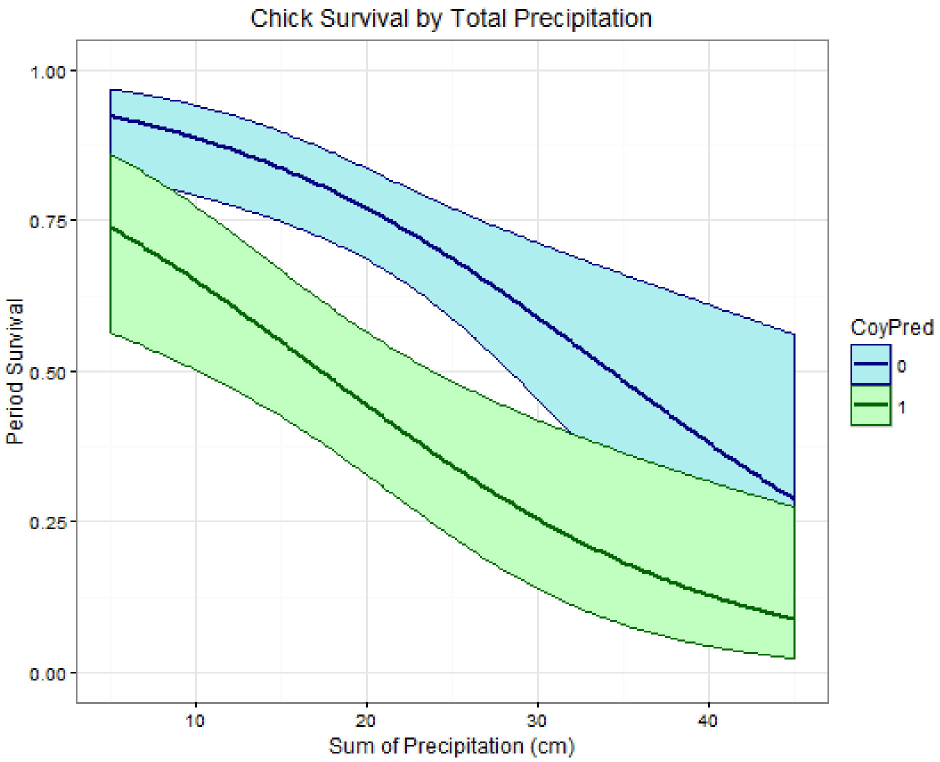

Figure 4.4: Predicted Wilson's Plover survival from top Cormack-Jolly-Seber model showing the effect of the total amount of precipitation on the period survival for chicks. The predicted chick survival with (green) and without (blue) coyote predation are also shown, with the 95% confidence interval shown around the mean prediction.

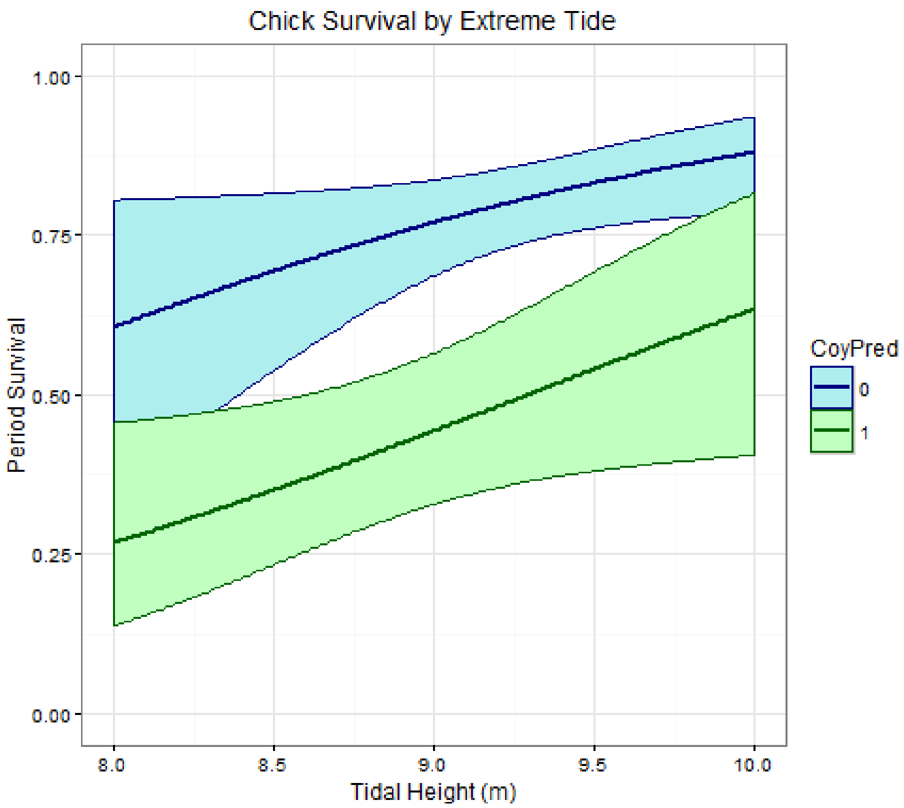

Figure 4.5: Predicted Wilson's Plover survival from top Cormack-Jolly-Seber model showing the effect of highest tide experienced by an individual during prefledging on the period survival for chicks. The predicted chick survival with (green) and without (blue) coyote predation are also shown, with the 95% confidence interval shown around the mean prediction.

CHAPTER 5

CONCLUSIONS AND FUTURE RESEARCH DIRECTIONS

Although the goal of this dissertation was to investigate factors that affect the productivity of American oystercatchers (*Haematopus palliatus)* and Wilson's plovers (*Charadrius wilsonia*) on barrier islands off the Georgia coast, another equally important overarching goal was to inform management efforts that could increase productivity of these two species of beach-nesting shorebirds. I found that the habitat features that predicted nest site selection were different from the habitat features that predicted nest success (Chapter 2). The mismatch between habitat cues that predict site selection and success has been documented in other systems (Kokko and Sutherland 2001, Schlaepfer et al. 2002, Battin 2004). This result suggests that basing management, such as predator control, only in areas with high nesting density rather than where nesting birds are more successful could increase the disconnect between informative habitat cues and successful habitat, potentially creating an ecological trap (Kristan 2003). Similarly, basing monitoring and survey protocols only where birds are commonly nesting might not provide an accurate estimate of overall productivity for a site (Vanhorne 1983, Cohen et al. 2009). These results also highlight that features from an intermediate scale, which approximated territory size, were more predictive than features at the microhabitat scale, quantified directly around a nest. Therefore managers can confidently make decisions using habitat features such as the community type, or even using aerial imagery, to evaluate potential nesting areas.

In part because habitat features were not as predictive of nest success as they were of nest location, I used competing risks models to understand how habitat might be influencing the risks of predation and overwash simultaneously for Wilson's plover nests (Chapter 3). Interestingly, habitat features were not at all predictive of nest predation, which was the major cause of nest failure. Overwash risk was predicted by habitat features, but there was a considerable amount of annual variability in overwash risk and the habitat features that were predictive of it. It appears that birds can be moderately successful when one or the other risk is high, but when both risks are elevated, productivity suffers. When overwash risk was increased, predation risk also increased and overall nest success was lowest, which could indicate that predator control efforts should be increased during times of high overwash. We also saw that predation had a significant impact on Wilson's plover chick survival (Chapter 4), which indicated that management actions should be applied during the entire breeding season, not only during nesting. While the effects of the novel predation pressure of coyotes (*Canis latrans*) could not be assessed directly for either nests or chicks, the models that I used did indicate that there was a potentially negative and additive impact of this non-native predator.

The other major objective of this research was to understand whether management actions focused on American oystercatchers also benefited Wilson's plovers, to better explore the role of American oystercatchers as an umbrella species for other beach-nesting birds. Focused management efforts within Georgia and across the breeding range, due to partnerships through the American Oystercatcher Working Group, have helped stop population declines for American oystercatchers, which adds support to single species conservation practices. However, the effectiveness of the umbrella species concept in conservation has been the subject of several recent reviews, and it is occasionally juxtaposed with the idea of multi-species management (Andelman and Fagan 2000, Roberge and Angelstam 2004). This dissertation highlighted that the removal of nest predators to increase success for oystercatchers would benefit not only Wilson's plovers, but other beach nesting species as well (McGowan et al. 2005, Pauliny et al. 2008, Martin et al. 2010, Schulte et al. 2010, Zdravkovic 2013). However, this research also suggests that broadening the focus of management planning from just one species like the American oystercatcher, to include others, such as Wilson's plovers, might be beneficial. For instance, the models for Wilson's plovers were better at predicting nest success than the models for American oystercatchers. At our sites, Wilson's plovers nested in greater densities, covered more of the landscape, and were likely closer to carrying capacity than American oystercatchers were. Because of this, it was easier to assess patterns between successful sites and habitat features; information that can be important to incorporate into management plans.

Another important reason to broaden from single species management to a multi-species approach is that, because American oystercatchers are long lived (Nol and Humphrey 2012) compared to Wilson's plovers and other beach nesting species in Georgia (Corbat and Bergstrom 2000), they may be more resilient to perturbations or stressors. Risks such as predation and overwash create a high amount of inter-annual variability of success, however even low rates of reproductive success might be enough to maintain the population of American oystercatchers because of their long lifespan (McGowan et al. 2005). However several years of reduced productivity might have very serious implications for a less long-lived species such as the Wilson's plover. It is my recommendation, therefore, that the focus of management be expanded to explicitly include Wilson's plovers and other beach nesting shorebirds, especially in light of increased challenges regarding novel predators, changing shorelines and increased abiotic stressors due to climate change.

There are several directions for future research that focus on increasing the understanding of these emerging threats including predation risk, as well as incorporating shoreline change dynamics into habitat models. Future research directed at assessing the impacts of specific predators, including investigating how predators with different foraging strategies, life-histories, and behavior influence predation risk, may be more informative than simply associating habitat features with predation risk (Cooper et al. 2015). As assemblages of predators shift, and novel predators enter a system, investigating not only how novel predators influence shorebird reproductive success but also how the population dynamics of novel predators interact with established predators will be useful as well (Harding et al. 2001, Clare et al. 2016). Modeling techniques such as agent-based models may be able to answer more questions about how predator behavior affects predation risk of nests (Ringelman 2014), which could be useful for guiding management and assessing how changing predator communities will influence shorebirds in the future. Additionally, predator removal is expensive and may not be sustainable indefinitely; future research that focuses on how and when to best employ strategies, and how the results of those strategies will influence target populations should be a priority as well.

Future research that focuses on shoreline change models, and integrates coastal geomorphology into predictions of changing shorebird habitat, can assist in identifying areas of high risk and vulnerability, especially in light of sea level rise due to climate change (Sims et al. 2013). Shoreline change analysis can identify erosional hotspots, predict how inlets change over time, identify areas of accretion, and reveal overall trends (Jackson 2015), all of which have implications for not only nesting habitat, but also for predicting roosting and foraging locations. Additionally, shoreline change models can be applied across both large and fine spatial scales, which makes them relevant for understanding changes that might have population level effects or have site specific implications. Finally, we need to continue studying how individuals respond to specific risks over time, which allows us to understand behavioral shifts in light of new threats to assess the adaptability of species (Lima 2009, Hunter et al. 2016). With detailed assessments of the factors that influence overall reproductive success, we can better understand the implications that a changing habitat has on the ability of these two species and other beach-nesting shorebirds to adapt and persist, and how management can facilitate these goals.

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